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# *The Bulletin of* MATHEMATICAL BIOPHYSICS

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*The BULLETIN is devoted to publications of research in Mathematical Biology, as described on the inside back cover.*

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## PROBABILITY THAT TWO DIFFUSING MOLECULES WILL COLLIDE

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A formula is derived for the probability  $P(r_1)$  that two molecules, originally at a distance  $r_1$  from each other and moving in an infinite scattering and absorbing medium, will eventually collide with each other.

The following problem, although physical in its statement, is important in its biological applications. Two molecules diffuse in an infinite scattering and absorbing medium; they will chemically react with each other if they ever happen to meet. Given the original separation, the problem is to find the probability that this reaction will have taken place after an infinite time has elapsed. This problem arises in the treatment of the "diffusion model" for the action of radiation on the genetic material of single cells. In this model the genetic damage is effected by ionization products, formed by the radiation anywhere in the cell and diffusing toward the genes, while being subject to the possibility of removal by undergoing chemical reactions with other cell constituents. Clearly, the probability that a certain gene will be damaged by such a diffusing ionization product constitutes a particular case of the problem stated above. Another application is found in the  $\text{H}_2\text{O}_2$  production in a liquid medium under the influence of radiation, where one  $\text{H}_2\text{O}_2$  molecule is formed by two OH radicals which approach each other by diffusion.

For the moment, we shall assume that the two molecules will react chemically at their first collision. The extension to the more general case, in which the reaction probability per collision is less than one, will be indicated later.

For simplicity, we shall assume that the two molecules are spherical in shape. The problem can be simplified, without loss of generality, by making one molecule stationary and letting only the other molecule diffuse, by assigning the latter the proper mean velocity and mean free path.

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Furthermore, we can consider the diffusing molecule as a point particle if we take the radius of the stationary molecule equal to the sum of radii of the original molecules.

The stationary molecule, with radius  $r_0$ , can be considered as a "black" sphere, i.e., a sphere which completely absorbs an incoming point particle. This sphere is surrounded by an infinite scattering and absorbing medium. If the point particle is initially at a distance  $r_1$  from the center of the black sphere, the problem is to find the probability  $P(r_1)$  that it will be caught by the sphere eventually. The answer to this problem is the same as the answer to the following spherically symmetric and time-independent problem. Given a source of one point particle per unit time distributed homogeneously over a spherical surface with radius  $r_1$  concentric with the black sphere, how can we calculate the number of point particles absorbed by the sphere per unit time? Thus formulated, the problem could apply to the diffusion of thermal neutrons in a scattering and absorbing medium.

As in neutron diffusion problems, we ignore the velocity distribution of the diffusing particles, and pretend that the particles move with a velocity  $v$ , which is constant in magnitude. Also, we assume that the scattering is isotropic. Let the mean free path for scattering be  $l$ , and let the probability per unit time that a particle will be absorbed by the medium be  $a$ . Each particle is characterized by its distance  $r$  to the center of the black sphere, and by the angle  $\theta$  between its velocity  $\vec{v}$  and the radius vector  $\vec{r}$ . Instead of  $\theta$ , we shall use  $\mu$ , where  $\mu = \cos \theta$ . We now introduce the function  $\psi(r, \mu)$ , so that  $4\pi r^2 \psi(r, \mu) dr d\mu$  is the number of particles between  $r$  and  $r + dr$  with velocity directions between  $\mu$  and  $\mu + d\mu$ . For  $\psi$  we can derive the Boltzmann transport equation†

$$v\mu \frac{\partial \psi}{\partial r} + v \frac{1 - \mu^2}{r} \frac{\partial \psi}{\partial \mu} + \frac{v}{l} \psi + a\psi - \frac{1}{2} \frac{v}{l} \psi_0 = \frac{1}{8\pi r_1^2} \delta(r - r_1), \quad (1)$$

in which

$$\psi_0(r) = \int_{-1}^1 \psi(r, \mu) d\mu$$

equals particle density at  $r$ , and  $\delta$  is the Dirac  $\delta$  function. In equation (1) the first two terms represent the loss of particles from interval  $dr d\mu$  as a result of their motion, the third term is the loss from collisions in  $dr d\mu$  to other intervals, the fourth term is the loss through absorption in the medium,

\* The writer is indebted to Dr. R. Serber for indicating the possibility of reduction to a time-independent problem.

† See, e.g., S. Chandrasekhar (1950).

the fifth is the gain from collisions in other intervals to  $drd\mu$ , and the right-hand side represents the spherical source at  $r = r_1$ . The calculations are simplified somewhat by introducing the dimensionless quantities

$$\rho = \frac{r}{l}, \quad \rho_1 = \frac{r_1}{l}, \quad \rho_0 = \frac{r_0}{l}, \quad \lambda = \frac{l}{v}a, \quad \varphi(\rho, \mu) = vl^2\psi(r, \mu). \quad (2)$$

With the substitutions (2), equation (1) is changed into

$$\mu \frac{\partial \varphi}{\partial \rho} + \frac{1 - \mu^2}{\rho} \frac{\partial \varphi}{\partial \mu} + (1 + \lambda) \varphi - \frac{1}{2} \varphi_0 = \frac{1}{8\pi \rho_1^2} \delta(\rho - \rho_1). \quad (3)$$

There are two boundary conditions. At  $\rho = \rho_0$  the requirement is that there are no particles coming out of the black sphere, and at  $\rho \rightarrow \infty$  the particle density should approach zero:

$$\varphi(\rho_0, \mu) = 0, \quad (\mu > 0), \quad (4)$$

$$\lim_{\rho \rightarrow \infty} \varphi(\rho, \mu) = 0. \quad (5)$$

The probability  $P(r_1)$  is obtained from the solution to equations (3), (4), and (5) as the total current entering the black sphere

$$P(r_1) = -4\pi r_0^2 v \int_{-1}^0 \psi(r_0, \mu) \mu d\mu,$$

and with the substitutions (2) we have:

$$P(r_1) = -4\pi \rho_0^2 \int_{-1}^0 \varphi(\rho_0, \mu) \mu d\mu. \quad (6)$$

Equations (3), (4), and (5) cannot be solved exactly, but R. E. Marshak (1947) has proposed a convenient approximate method, called the "Spherical Harmonic Method," which we shall use in our problem. The method consists of expanding  $\varphi(\rho, \mu)$  in a series of Legendre polynomials  $P_l(\mu)$ :

$$\varphi(\rho, \mu) = \sum_l (l + \frac{1}{2}) \varphi_l(\rho) P_l(\mu),$$

and breaking the series off after a finite number of terms. We shall only keep the first two terms

$$\varphi(\rho, \mu) = \frac{1}{2} \varphi_0(\rho) + \frac{3}{2} \varphi_1(\rho) \mu, \quad (7)$$

calling this the " $P_1$ -approximation." The validity of this approximation will be discussed later. After substituting (7) into (3), applying the operations

$$\int_{-1}^1 d\mu \quad \text{and} \quad \int_{-1}^1 \mu d\mu$$

respectively on both sides of the equation, we obtain two equations for  $\varphi_0$  and  $\varphi_1$ :

$$\lambda \varphi_0 + \frac{d\varphi_1}{d\rho} + 2 \frac{\varphi_1}{\rho} = \frac{1}{4\pi\rho_1^2} \delta(\rho - \rho_1), \quad (8)$$

$$(1 + \lambda) \varphi_1 + \frac{1}{3} \frac{d\varphi_0}{d\rho} = 0. \quad (9)$$

In the Spherical Harmonic Method it is impossible to satisfy boundary condition (4) exactly. In the  $P_1$ -approximation, for instance, (4) would read:  $\varphi_0(\rho_0) = 0$ ,  $\varphi_1(\rho_0) = 0$ , but in order to find solutions of (8) and (9) we can allow only one boundary condition at  $\rho_0$ . With Marshak, we choose for this boundary condition the requirement that the total current leaving the black sphere be zero. Thus we replace (4) by

$$\int_0^1 \varphi(\rho_0, \mu) \mu d\mu = 0. \quad (10)$$

Substitution of (7) into (10) and (5) gives the boundary conditions

$$\frac{1}{2} \varphi_0(\rho_0) + \varphi_1(\rho_0) = 0, \quad (11)$$

$$\lim_{\rho \rightarrow \infty} \varphi_0(\rho) = 0, \quad \lim_{\rho \rightarrow \infty} \varphi_1(\rho) = 0. \quad (12)$$

After elimination of  $\varphi_1$  we can solve for  $\varphi_0$  with the following result:

$$\begin{aligned} \rho \varphi_0(\rho) = \frac{\sqrt{3}}{8\pi\rho_1} \sqrt{\frac{1+\lambda}{\lambda}} \left\{ e^{-\sqrt{3\lambda(1+\lambda)}|\rho-\rho_1|} \right. \\ \left. + \frac{\sqrt{3\lambda(1+\lambda)} - \frac{3}{2}(1+\lambda) - \frac{1}{\rho_0}}{\sqrt{3\lambda(1+\lambda)} + \frac{3}{2}(1+\lambda) + \frac{1}{\rho_0}} e^{-\sqrt{3\lambda(1+\lambda)}(\rho+\rho_1-2\rho_0)} \right\}. \end{aligned} \quad (13)$$

If we substitute (7) into (6) and keep in mind (11), we obtain  $P(r_1) = 2\pi\rho_0^2\varphi_0(\rho_0)$ . Evaluating (13) at  $\rho = \rho_0$  we finally obtain:

$$P(r_1) = \left( 1 + \frac{2}{\sqrt{3}} \sqrt{\frac{\lambda}{1+\lambda}} + \frac{2}{3\rho_0(1+\lambda)} \right)^{-1} \frac{\rho_0}{\rho_1} e^{-\sqrt{3\lambda(1+\lambda)}(\rho_1-\rho_0)}. \quad (14)$$

It is seen from (2) that  $\lambda$  is the ratio of mean free path for scattering to mean free path for absorption. Since in most of the interesting cases the number of absorbing molecules is small compared to the number of scattering molecules, we may assume  $\lambda \ll 1$ . If we neglect  $\lambda$  compared to unity in equation (14), change back to the original variables by means of

(2), and introduce  $D = \frac{1}{3}vl$ , which has the dimension of a diffusion constant, the final result is

$$P(r_1) = \left(1 + \frac{2l}{3r_0}\right)^{-1} \frac{r_0}{r_1} \exp \left[ -\sqrt{\frac{a}{D}}(r_1 - r_0) \right]. \quad (15)$$

The dependence of  $P(r_1)$  on  $r_1$  is two-fold:  $P(r_1)$  is inversely proportional to  $r_1$  as a result of diffusion alone, and proportional to an exponential in  $r_1$  as a combined result of diffusion and absorption.

If we want to calculate the probability that the two molecules will chemically react in case the reaction probability per collision is less than one—say,  $1 - \alpha$ —we have to replace the “black” sphere by a partially reflecting sphere. Equations (8) and (9) will still be valid, but the boundary condition (10) has to be replaced by the requirement that the current emerging from the sphere is a fraction  $\alpha$  of the current entering the sphere:

$$\int_0^1 \varphi(\rho_0, \mu) \mu d\mu = -\alpha \int_{-1}^0 \varphi(\rho_0, \mu) \mu d\mu.$$

If the calculation is carried through, it is found that the result is given by (15), except that the factor

$$\left(1 + \frac{2l}{3r_0}\right)^{-1}$$

has to be replaced by

$$\left(1 + \frac{2l}{3r_0} \frac{1+\alpha}{1-\alpha}\right)^{-1}.$$

*Validity of the approximation.* If  $l \ll r_0$ , equation (15) simplifies to

$$P(r_1) = \frac{r_0}{r_1} \exp \left[ -\sqrt{\frac{a}{D}}(r_1 - r_0) \right],$$

a result which can be obtained in a much simpler way from the solution of a differential equation rather than the Boltzmann transport equation. The purpose of the method of solution used in this paper is to obtain the extra factor

$$\left(1 + \frac{2l}{3r_0}\right)^{-1}$$

in case  $l$  is not much less than  $r_0$ . It still remains to be shown what the domain of validity of equation (15) is. Since the extra factor is independent of the absorption in the medium, we may take  $a = 0$ , which simplifies the calculation. After the  $P_2$ -approximation is carried out, it turns out that the factor

$$\left(1 + \frac{2l}{3r_0}\right)^{-1}$$

has to be replaced by

$$\left(1 + \frac{2l}{3r_0} + \frac{l^2}{2r_0^2}\right)^{-1}.$$

It is clear then that the result of the  $P_1$ -approximation is not valid for values of  $l \geq r_0$ , but gives a reasonably good approximation if  $l < r_0$ .

The author wishes to thank Dr. Herbert D. Landahl for valuable suggestions concerning the way of presentation.

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## THE LIMITING INFORMATION CAPACITY OF A NEURONAL LINK

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The maximum rate at which a synaptic link could theoretically transmit information depends on the type of coding used. In a binary modulation system it depends chiefly on the relaxation time, and the limiting capacity equals the maximum attainable impulse rate. In a system using pulse-interval modulation, temporal precision may be a more important limiting factor. It is shown that in a number of typical cases a system of the second type could transmit several times more information per second through a synaptic link than a binary system, and the relation between relative efficiency, relaxation-time, and temporal resolving power is generalized in graphical form. It is concluded, not that interval modulation rather than binary modulation "ought" to be the mode of action of the central nervous system, but that the contrary assumption is unsupported by considerations of efficiency.

*I. Introduction.* The way in which the nervous system transmits information has long been the subject of debate. On the one hand, the all-or-none character of the nervous impulse and the demonstrated performance of motoneurons as coincidence detectors (Lorente de Nó, 1939) led naturally first to a model of the central nervous system (McCulloch, 1943; Pitts and McCulloch, 1947) in which information was represented in terms of binary digits, quantized with respect to time as in a serially operated digital computer. On the other hand, there has been a steady accumulation of other evidence which has been adduced in favor of models (Lashley, 1942) employing frequency modulation of trains of impulses to represent the information transmitted. We refer here not only to the long known fact that sense organs deliver trains of impulses whose frequency after adaptation is roughly proportional to the logarithm of the intensity of stimulation, but also more particularly to recent observations (Brookhart, Moruzzi and Snider, 1950; Gernandt, 1950) that the frequency of discharge of spontaneously active central neurons can be altered in response to signals afferent to them.

In view of these last observations and others like them, it seems realistic

to consider how efficiently a typical neuronal link, or "synapse," could be used to convey information in this way, and particularly to compare its limiting efficiency with that which could be achieved if it were used on the digital basis of the first model.

It is not to be expected that the proponents of either of these models believed them to be the whole story, nor is it our purpose in the following investigation to reopen the "analogical versus digital" question, which we believe to represent an unphysiological antithesis. The statistical nature of nervous activity must preclude anything approaching a realization in practice of the potential information capacity of either mechanism, and in our view the facts available are inadequate to justify detailed theorization at the present time. What does seem worth while at the moment is a sufficiently general discussion to determine upper limits of performance and so provide a quantitative background to lend perspective to the framing of hypotheses.

*II. Selective information content.* A signal is a physical event that, to the receiver, was not bound to happen at the time or in the way it did. As such, we may think of it as one out of a number of possible alternative events, each differing perceptibly in some respect from all the other possibilities. A given signal can therefore be considered as an indicator, selecting one out of a finite number of perceptibly distinct possibilities, and thus indicating something of the state of affairs at its point of origin. The greater the number of possible alternatives to a given signal, the greater the "amount of selective information" we say it contains. The selective information-content of a signal is in fact defined as the logarithm (base 2) of the number of alternatives, where these are all equally likely a priori. This simply represents the number of steps in a search process among the alternatives carried out in the most efficient way—by successive subdivision of the total assembly into halves, quarters, and so forth. (We shall not consider the case of unequal prior probabilities.)

Now a neuronal impulse carries information, in the sense that it indicates something of the state of affairs at its point of origin. It is able, moreover, on arriving at an axonal termination, to affect the probability of occurrence of an impulse in the axon of the cell with which it "synapses." Thus, whatever else does or does not "cross a synapse," it is safe to say that information does. The nature or even the existence of the synapse as a physical link is not here in question. For our purpose it will be sufficient to consider the observable time-relations which obtain between incoming and outgoing impulses in cases in which these are temporally coherent. These will enable us to estimate the upper limits to the informa-

tion capacity of such synaptic links—the maximum number of “bits” carried per second—and to compare the informational efficiencies of the different modes of operation (called modulation systems by the communication engineer) which are conceivably available to model makers of the C.N.S.

In particular we shall examine the suggestion that an all-or-none binary code using pulses separated by minimal quantized time intervals would be more efficient than a system using the same elements in which the varying time of occurrence of impulses represented the information to be conveyed. This does not appear to be the case.

*III. The selective information-content of an impulse.* To determine the limiting information-content of a signal, we have to decide (a) which parameters are permissible variables, (b) how large a variation must be in

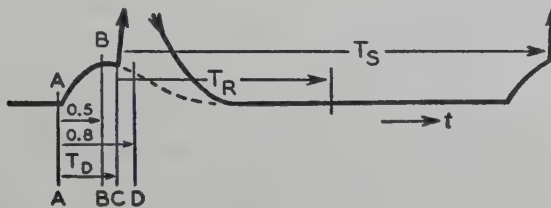


FIGURE 1

order to be perceptible, or rather to be statistically significant, and hence (c) how many significantly distinct values of each parameter are possible. We ought also to know (d) the relative probabilities of the different possible combinations of parametric values, if these probabilities are unequal; but unless their differences are great the order of magnitude of the information content will not be affected. (The effect will always be a reduction of the average information-content per signal.)

The limiting *selective information-capacity* of a signal-carrying element will then be the product of the average information-content per signal, with the maximum mean signal-frequency allowable for the modulation-system adopted.

Typical time-relations which have been observed in so-called synaptic transmission are summarized in Figure 1.

An afferent impulse which begins to rise at *A* may give rise to a spike (of about 1 msec. in duration) at any time *C* between *B* and *D*, 0.5 to 0.8 msec. later. The majority of spikes, however, are observed to occur after an interval, the “synaptic delay,”  $T_D$ , with a standard deviation of less than 0.05 msec., and a typical mean value of the order of 0.65 msec. (Lloyd, 1946).

No matter how high the frequency of stimulation, successive spikes are not observed to occur within time intervals  $T_s$  of less than 1 msec. Frequencies of 500 per second are not long sustained, and a reasonable upper limit for a steady response to recurrent stimuli would perhaps be 250 per second. In central auditory nerve fibers for which unfortunately no constants of monosynaptic transmission are available to us, maximum frequencies, after adaptation, of 250 to 300 c/s have been observed (Galambos and Davis, 1943). There is thus a minimal "dead time"  $T_R$  between impulses which ranges from 1 to 4 msec., according to the demands made on endurance.

Now the amplitude of a nerve impulse is relatively slowly variable, and the total amount of information conveyable by such variation would be relatively small. For our purpose we shall assume that the amplitude can have only two values, namely, zero or unity on an *ad hoc* scale. Thus each impulse, simply by its presence or absence during the short period over

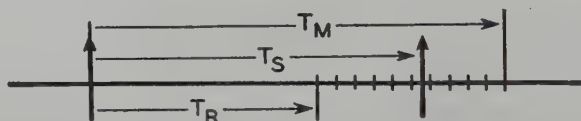


FIGURE 2

which it was expected, could provide one unit or "bit" of selective information. If, therefore, we had a system in which we "quantized" the time scale by dividing it into discrete intervals equal to the minimum necessary separation  $T_R$  between impulses, the system should on the above basis be able to convey  $1/T_R$  bits of information per second at most. Such a system we may call a time quantized binary system (McCulloch and Pitts, 1943).

There is, however, another variable parameter of our neuronal signal. The *time interval* between successive impulses can vary, so that any given interval represents a choice out of a certain range of possible pulse positions on the time axis. Let us denote by  $T_s$  the time interval between one pulse and its immediate predecessor (Fig. 2), and suppose that for reasons which we consider later  $T_s$  has a maximum permissible value  $T_M$ , and of course a minimum  $T_R$ . The range of  $T_s$ ,  $(T_M - T_R)$ , may be thought of as subdivided into a finite number of equal intervals, of magnitude  $\Delta T$ .

These intervals must not be smaller than the average fluctuations in  $T_D$  (Fig. 1) if changes in  $T_s$  are to be statistically significant, and we may conveniently assume at first that they are of the order of 0.05 msec. (Lorente de N3, *loc. cit.*, p. 409). We thus think of our impulse as selecting,

by its occurrence at  $T_s$ , one out of  $(T_M - T_R)/\Delta T$  possible positions on the time axis. Calling the ratio  $(T_M - T_R)/\Delta T$ ,  $n$ , we have here  $\log_2 n$  bits of selective information per signal, in respect of its instant of occurrence.

Now for maximum efficiency our hypothetical system should on an average use all  $n$  possible values of  $T_s$  equally frequently. The mean value of  $T_s$  will therefore at maximum efficiency be  $\frac{1}{2}(T_M + T_R)$ . A "pulse interval modulation" system could evidently convey in this way a maximum of

$$C = \frac{2}{T_M + T_R} \log_2 n$$

bits of information per second.

It is here that we find a criterion for the optimum value of  $T_M$ . Clearly if  $T_M$  is allowed to increase indefinitely, the number of bits per impulse also increases indefinitely—but only roughly as the logarithm of  $T_M$ , whereas the number of impulses per second goes down roughly as the inverse of  $T_M$  itself. The optimum value of  $T_M$  is that which maximizes

$$C = \frac{2}{T_M + T_R} \log_2 \frac{T_M - T_R}{\Delta T}. \quad (1)$$

If we take  $\Delta T$  as our unit of time, writing  $T_M = m\Delta T$  and  $T_R = r\Delta T$ , we have

$$C = \frac{2}{\Delta T (m + r)} \log_2 (m - r). \quad (2)$$

This is maximum for a given  $r$  when

$$\frac{m + r}{m - r} = \ln (m - r). \quad (3)$$

Taking a value of 1 msec. for  $T_R$  and 0.05 msec. for  $\Delta T$ , we find by approximate solution of (3) that at  $T_M = 2$  msec. a maximum selective information capacity of about 2.9 bits per msec. could theoretically be attained, as against 1 bit per msec. on the binary quantized system. Under these conditions the mean frequency would be about 670 impulses per second and the average information content about 4.3 bits per impulse.

*IV. First approximations to realism.* Our discussion hitherto has been mainly academic. We have seen that a communication engineer could use an element with the properties idealized in Figure 1, nearly three times as efficiently in a pulse-interval modulation system as in a binary system at the maximum possible pulse frequency. We have favored the latter as much as possible by (a) granting a maximum frequency of 1000

per second; but (b) we have not yet asked whether the precision of timing between stimulus and outgoing impulse is matched by a corresponding precision of time-resolution in possible receiving centers; (c) we have not considered the possible increase in the variance of synaptic delay due to irregularity in the pulse sequence; and (d) we have assumed all values of the modulated pulse-interval to be equally likely, irrespective of the position of its predecessor. This last assumption is valid in an estimate of *limiting capacity*.

In other words, our computation is probably not too unrealistic as an estimate of the maximum number of bits per msec., or even per 10 msec., which could be represented by the physical behavior of the signal. But for an estimate of the information effectively carried we must, as we saw above, consider the number of possibilities distinguishable by the receiver; and for an estimate of continuous information-capacity we must accept a lower value for the mean impulse-frequency.

Information on points (b) and (c) is scanty. It is known (Lorente de Nó, *loc. cit.*, p. 422) that the period of latent addition of two converging impulses, over which their relative arrival-time may vary without appreciable effect, is of the order of 0.15 msec. This might seem to suggest that our scale unit of time  $\Delta T$  should be of the same magnitude, or even twice this, since the relative delay may be of either sign. But the index of latent addition falls off very sharply over a few hundredths of a millisecond when the relative delay exceeds 0.15 msec. As a time resolving instrument, therefore, such a summation mechanism can in principle detect coincidence to much finer limits (as may be seen by imagining a constant delay of 0.15 msec. to be introduced into one signal path), so that it is not obvious that the operational value of  $\Delta T$  merits much increase.

Not much more is known about the effects of irregular firing on synaptic delay. A range of 0.4 msec. is given by D. Lloyd (*loc. cit.*) as the difference between the delay measured for a relatively refractory neuron which had just fired, and that for a relatively excitable neuron receiving summing impulses. In the case we have considered above, which is relatively least favorable to interval modulation, the interval between successive pulses might vary from 1 msec. to 2 msec. and might reasonably be expected to affect synaptic delay by perhaps 0.1 to 0.2 msec.

Let us suppose for a moment that in the worst case an imprecision  $\Delta T$  of 0.3 msec. had to be accepted, and that we again tolerate a minimum pulse to pulse interval of 1 msec. The same calculation as before shows that at the optimum value of  $T_M$  around 3.1 msec., an average information capacity of some 1.4 bits per msec. would be attainable, so that

even under these extreme conditions a binary system would still be less efficient than the other by 40 per cent.

We must, however, make a further step toward realism by estimating the capacities for a higher value of the refractory period  $T_R$ . Taking a frequency of 250 per second as reasonably attainable after adaptation (Galambos and Davis, *loc. cit.*) we can set  $T_R = 4$  msec. as perhaps a typical "adapted" value. We then find that when  $\Delta T = 0.05$  msec. the optimum value of  $T_M$  is 6.6 msec. and the optimum mean frequency 190 per second, yielding as much as 1090 bits per second or nearly 6 bits per impulse. (At the maximum possible rate of 250 per second the corresponding capacity on a digital basis is of course only 250 bits per

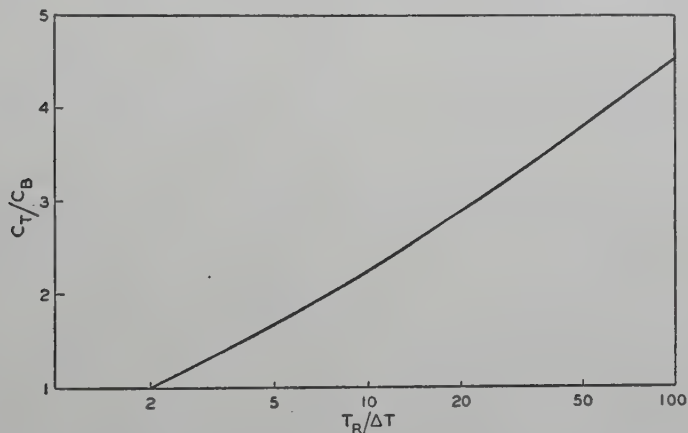


FIGURE 3. Relative efficiency of interval and binary modulation

second.) Even if  $\Delta T$  must be as large as 0.3 msec., a capacity of 620 bits/sec. can be attained at  $T_M = 8.6$  msec. and a mean frequency of 160 per second—still  $2\frac{1}{2}$  times the maximum capacity of the same element used in a binary system. Figure 3 shows in general how the ratio of the information capacity with interval modulation ( $C_T$ ) to that with binary modulation ( $C_B$ ) varies with the ratio  $T_R/\Delta T$ .

Turning finally to consider normal as opposed to optimal conditions, we may take 50 impulses per second as a typical mean frequency of excitation of sensory fibers when transmitting information. Our calculation is now straightforward. A mean pulse to pulse interval of 20 msec. could correspond roughly to a minimum  $T_M$  of (let us say again) 4 msec., and a maximum of 36 msec.—a range of 32 msec. Each impulse then selects one out of  $32/\Delta T$  possible positions, so that if  $\Delta T$  were taken as 0.05 msec., the selective information content of each impulse would be  $\log_2 640$  or about

9.3 bits per impulse, giving an information capacity of just under 500 bits per second despite the low impulse repetition frequency.

In general if a different value be taken for  $\Delta T$ , say  $k$  times greater ( $T_M$  and  $T_R$  remaining the same), the effect is to reduce the selective information content per impulse by  $\log_2 k$ . Thus an increase of  $\Delta T$  to 0.2 msec. allows only 7.3 bits per impulse; an increase to 0.4 msec., 6.3 bits, and so on. It should be noted, however, that these are figures for a fixed value of  $T_M$  and are not the maximum figures for each value of  $\Delta T$ , which would be determined by optimizing  $T_M$  as in the preceding sections.

It is of course exceedingly unlikely in practice that successive impulse positions would be statistically uncorrelated in these cases where so large a percentage change is theoretically possible in successive pulse intervals. It should be noted moreover that we have considered only one synaptic link. If a number of these were connected in series, the precision of timing would of course diminish, roughly as the square root of the number of links. Our qualitative conclusions should hold however for reasonably large multisynaptic links, since, as shown in Figure 3, the interval modulation system does not become inferior to the binary until  $\Delta T$  exceeds  $\frac{1}{2}T_R$ .

*V. Conclusions.* Our discussions have here been concerned with the *limiting* capacity of a neuronal link as a transducer of information. We have seen that the observed time-relations between incoming and outgoing impulses indicate a precision that would justify the use of pulse interval or "frequency" modulation rather than binary all-or-none amplitude modulation in a communication system using such a transducer.

At the maximum pulse frequency normally attainable, the binary system would be inferior to the other by a factor of 2 or 3 at least. At the typical peripheral frequency of 50 per second, the theoretical factor in favor of interval modulation rises to 9 or more. Little significance is attached to the precise figures obtained, but they indicate the theoretical possibility that a maximum of between 1000 and 3000 bits per second could be transferred at a synaptic link.

It appears to the writers at least that the question is still mainly of academic interest. Its discussion must not be taken to imply a belief that either binary coding or pulse-interval coding in the communication engineer's sense are the modes of operation of the central nervous system. Much more likely is it that the statistically determined scurry of activity therein depends in one way or another on *all* the information-bearing parameters of an impulse—both on its presence or absence as a binary digit and on its precise timing and even its amplitude, particularly on the *effective* amplitude as modified by threshold control, proximity effects and

the like. If cerebral activity is the stochastic process it appears to be, the informationally significant descriptive concepts when once discovered seem likely to have as much relation to the parameters defining the states of individual neurons, as concepts such as entropy and temperature have to the motions of individual gas molecules—and little more.

Perhaps the most realistic conclusion is a negative one. The thesis that the central nervous system “ought” to work on a binary basis rather than on a time-modulation basis receives no support from considerations of efficiency as far as synaptic circuits of moderate complexity are concerned. What we have found is that at least a comparable information capacity is potentially available in respect of impulse timing—up to 9 bits per impulse in the cases we considered—and it seems unlikely that the nervous system functions in such a way as to utilize none of this. It is considered equally unlikely that its actual mode of operation closely resembles either form of communication system, but this quantitative examination may perhaps serve to set rough upper limits and to moderate debate.

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## THE PROBLEM OF EXCHANGE BETWEEN TWO OR MORE INDIVIDUALS, MOTIVATED BY HEDONISTIC CONSIDERATIONS

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Let two or more individuals each possess different quantities of two objects of satisfaction. Under certain conditions they may agree to exchange part of the objects if this leads to an increase of each one's satisfaction. The equations which govern this process have been derived by G. E. Evans (1930) for the case of two individuals. A different proof of these equations is given here and the equations are generalized to the case of more than two individuals.

The problem which we are going to discuss originated in economics, though it is of importance in more general social problems. We are concerned with two individuals who possess corresponding amounts  $a_1$  and  $a_2$  of one commodity, and  $b_1$  and  $b_2$  of another commodity. These individuals may trade the two commodities in such a way that after exchange they correspondingly possess the amounts  $x_1$  and  $x_2$  of the first commodity and  $y_1$  and  $y_2$  of the second. We then have

$$x_1 + x_2 = a_1 + a_2 ; \quad (1)$$

$$y_1 + y_2 = b_1 + b_2 . \quad (2)$$

The problem is to determine the values  $x_1$ ,  $x_2$ ,  $y_1$ , and  $y_2$ . Evans (*loc. cit.*, pp. 125–28) has given a solution of the problem based on considerations of the utility function. His proof, semi-geometric, is somewhat involved and is not readily generalized to several individuals.

In our previous work (Rashevsky, 1947, 1951) we used the concept of satisfaction function, which at least formally is identical with the utility function of the economist. We shall now give a proof of Evans' solution in what we believe is a simpler way, and shall indicate its generalization to more than two individuals and more than two commodities; or, as we prefer to call them in a more general way, objects of satisfaction.

Denote the satisfaction functions of the two individuals correspondingly by

$$S_1(x_1, y_1); \quad S_2(x_2, y_2). \quad (3)$$

Let the two individuals trade the two objects at a constant "price"  $p$ , so that if, say, the first one gives away an amount  $dx_1$  of  $x_1$  and receives in return an amount  $dy_1$  of  $y_1$ , then always

$$\frac{dy_1}{dx_1} = \frac{dy_2}{dx_2} = -p. \quad (4)$$

Since  $p$  is constant, therefore this implies

$$\frac{y_1 - b_1}{x_1 - a_1} = \frac{y_2 - b_2}{x_2 - a_2} = -p. \quad (5)$$

The first individual will be willing to trade as long as by giving away an amount  $dx_1$  and receiving an amount  $dy_1 = -pdx_1$  his  $S_1(x_1, y_1)$  is increased. The change of  $S_1$  due to giving away an amount  $dx_1$  is equal to

$$\frac{\partial S_1}{\partial x_1} dx_1, \quad (6)$$

whereas the change of  $S_1$  due to receipt of  $dy_1$  is equal, because of equation (4), to

$$\frac{\partial S_1}{\partial y_1} dy_1 = -p \frac{\partial S_1}{\partial y_1} dx_1. \quad (7)$$

Hence the first individual will trade as long as  $dS > 0$ . Because of  $dx_1 < 0$  this implies

$$\frac{\partial S_1}{\partial x_1} - p \frac{\partial S_1}{\partial y_1} < 0. \quad (8)$$

His satisfaction function  $S_1$  will be at a maximum for such values of  $x_1$  and  $y_1$  for which

$$\frac{\partial S_1}{\partial x_1} = p \frac{\partial S_1}{\partial y_1}. \quad (9)$$

By a similar argument we find that the second individual will trade until

$$\frac{\partial S_2}{\partial x_2} = p \frac{\partial S_2}{\partial y_2}. \quad (10)$$

A complete agreement will be reached if, and only if, both (9) and (10) are satisfied. Putting

$$\frac{\partial S_1}{\partial x_1} = X_1; \quad \frac{\partial S_1}{\partial y_1} = Y_1; \quad \frac{\partial S_2}{\partial x_2} = X_2; \quad \frac{\partial S_2}{\partial y_2} = Y_2; \quad (11)$$

we see that the values  $x_1$ ,  $x_2$ ,  $y_1$ , and  $y_2$ , for which neither individual will want to trade any further, satisfy the equations:

$$X_1(x_1, y_1) = p Y_1(x_1, y_1); \quad (12)$$

$$X_2(x_2, y_2) = p Y_2(x_2, y_2). \quad (13)$$

Together with equations (1), (2), and (5) we have five independent equations for the determination of the five variables  $x_1$ ,  $x_2$ ,  $y_1$ ,  $y_2$ , and  $p$ .

Eliminating  $p$  from equations (5), (12), and (13), and making use of (1) and (2), we find:

$$\frac{X_1(x_1, y_1)}{X_2(a_1 + a_2 - x_1, b_1 + b_2 - y_1)} = \frac{Y_1(x_1, y_1)}{Y_2(a_1 + a_2 - x_1, b_1 + b_2 - y_1)} \quad (14)$$

and

$$\frac{y_1 - b_1}{x_1 - a_1} = -\frac{X_1(x_1, y_1)}{Y_1(x_1, y_1)}. \quad (15)$$

Equations (1), (2), (14), and (15) determine  $x_1$ ,  $x_2$ ,  $y_1$ , and  $y_2$ . They are identical with those given by Evans.

This derivation is easier to generalize for the case of three or more individuals trading only two objects of satisfaction, than is the derivation given by Evans. For three individuals we have:

$$x_1 + x_2 + x_3 = a_1 + a_2 + a_3, \quad (16)$$

$$y_1 + y_2 + y_3 = b_1 + b_2 + b_3, \quad (17)$$

and

$$\frac{dy_1}{dx_1} = \frac{dy_2}{dx_2} = \frac{dy_3}{dx_3} = -p. \quad (18)$$

Putting

$$\frac{\partial S_1}{\partial x_1} = X_1, \quad \frac{\partial S_1}{\partial y_1} = Y_1, \quad (19)$$

we now find, by the same argument as before:

$$\begin{aligned} X_1(x_1, y_1) &= p Y_1(x_1, y_1); & X_2(x_2, y_2) &= p Y_2(x_2, y_2); \\ X_3(x_3, y_3) &= p Y_3(x_3, y_3). \end{aligned} \quad (20)$$

From equation (18) we have

$$\frac{y_1 - b_1}{x_1 - a_1} = \frac{y_2 - b_2}{x_2 - a_2} = \frac{y_3 - b_3}{x_3 - a_3} = -p. \quad (21)$$

Only two of the equations (21) are independent, because of equations (16) and (17). Thus we have seven equations to determine the seven variables  $x_1$ ,  $x_2$ ,  $x_3$ ,  $y_1$ ,  $y_2$ ,  $y_3$ , and  $p$ .

An interesting generalization is suggested by considering  $p$  not as con-

stant, but as a function of  $x_1$  and  $y_1$  in the case of two individuals. Instead of equation (5) we now shall have a more general expression of the form

$$P(x_1, y_1) = \text{Const.} \quad (22)$$

If  $p(x_1, y_1)$  is prescribed, we proceed as before. We may however attempt to determine such a form of  $p(x_1, y_1)$  which, for instance, gives a largest possible value to either  $S_1$ ,  $S_2$ , or  $S_1 + S_2$  after the trading is completed.

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## COMMUNICATION IN A HIERARCHICAL NETWORK

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An analogy is drawn between a hierarchical communication network and a pyramidal election system. An equation is derived relating the probability that a given person will vote for an issue to the probability that the elected officer will also vote for that issue. The equation contains the size of the population, the required majority ratio, and the number of stages in the election system as parameters.

Such an election system is compared to the simple majority vote without a hierarchy. The absence of a hierarchy appears to favor the minority voice.

All of the results are translatable into the language of neural nets.

Neural nets, groups of cooperating individuals, computing machines, and a great variety of other phenomena can be thought of as *connected systems of elements transmitting certain changes of state*. It is not surprising, therefore, that the language and nomenclature of these various phenomena are to some extent interchangeable. Furthermore, as we might also expect, certain quantitative relations seem common to all of them. Thus, some of the mathematical formulations, though couched in the terminology of neural nets, have interesting implications in the theory of epidemics.

The use of a specific terminology may, if taken too seriously, divert our attention from the more general aspects of the mathematical formulations. It may, on the other hand, serve as an intuitive guide in developing the equations. In this paper the terminology of neural nets will be emphasized, but some other interpretations will also be given.

Communication networks can be divided into two broad classes—those which contain closed loops (feed-back systems) and those which do not contain closed loops. An interesting example of the second category is the hierarchical structure.

Hierarchical structures have been met in the theory of neural ontogeny (Shimbel, 1948, 1950; Rapoport and Solomonoff, 1950).

Figure 1 is an example of a hierarchical communication net. In particu-

lar, we may think of it as a group of interconnected neurons, the heavy dots representing the cell bodies and the arrows their axones. The axones of the outermost cell bodies are seen to converge in groups of four to the cell bodies of "higher order" neurons in a circle just inside of the peripheral one. This process is repeated until the axones of the innermost circle converge upon a single "master neuron" located at the center.

The circular arrangement of neurons (or, more generally, *elements*) used in Figure 1 to illustrate the hierarchical structure is arbitrary. Pyramidal and tree-like arrangements would be completely equivalent so long as the

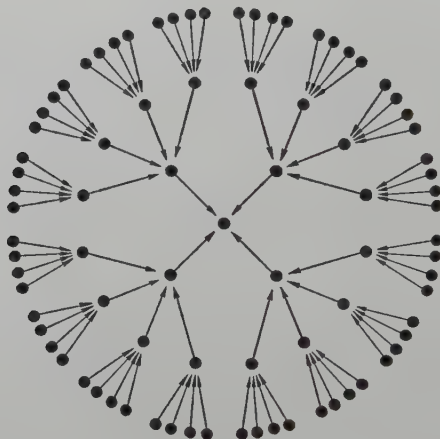


FIGURE 1

order of the connections was not disturbed. The important thing here is not the geometry, but the hierarchical "topology" of the system.

Let us suppose that the master neuron receives axones from  $a$  different neurons (on the innermost circle), and that each of these receives axones from  $a$  different neurons from the next circle, and so on. Now, if we trace any pathway from a peripheral neuron to the master neuron, we will in general make contact with  $K$  neurons (including the master neuron), where  $K$  is the number of concentric circles in the hierarchical diagram. Each neuron in the system can, therefore, be thought of as a member of a "stage" of the hierarchy. The stages can be numbered from zero (the outermost circle) to  $K$  (the master neuron).

In general, any neuron in the system will fire if it is sufficiently stimulated by its subordinates (those neurons which send axones to it). The

number of subordinates which must act together (within the period of latent addition) in order to comprise a sufficient stimulus may be thought of as the threshold  $\alpha - \beta$  of the neuron, where  $\beta$  is the maximum number of subordinates which may fail to fire during a sufficient stimulation. The peripheral cell bodies receive no axones and must, therefore, be thought of as receptors.

In particular, we may suppose that the receptors are photo-sensitive and that they have been exposed to a uniform field of light for a brief interval of time (less than the period of latent addition). This stimulus will cause some of the receptors (those which have absorbed enough energy) to fire. The number of receptors to become so activated will, of course, depend upon the intensity of the stimulus.

If the intensity is sufficiently high, then the probability that a large number of the receptors will fire is also high. This would result in the effective stimulation of the more central neurons, which after  $K$  stages would bring the master neuron into activity.

Conversely, for low stimulus intensities, we should expect that only a few of the receptors would be activated, so that correspondingly fewer central neurons would come into play, thus greatly reducing the probability that the master neuron will eventually be fired.

Let us denote with  $p_k$  the probability that a randomly selected neuron of the  $k$ th stage is eventually brought into activity as a consequence of such an initial stimulation of the peripheral receptors. Similarly, we shall denote by  $p_K$  the probability that the master neuron will fire, and by  $p_0$  the probability that any given receptor will fire. Our first problem is to determine the relation which must exist between  $p_K$  and  $p_0$ .

Note that any neuron of the  $k$ th stage will fire if, and only if,  $\alpha - \beta$  or more of its subordinate neurons have fired. (They must necessarily be in phase, because of the brief stimulation period.) This, however, can happen in a great many different ways.

It could happen, for example, that all of the subordinate neurons fire. (This could occur in only one way.) It could also happen that all but one of the subordinates fire (that is,  $\beta = 1$ ). In the latter case the failing neuron could be any one of the  $\alpha$  subordinates.

Now, in general,  $i$  of the subordinates can *fail* to fire, where  $i$  is any integer smaller than or equal to  $\beta$ . These  $i$  failing neurons can be chosen among the  $\alpha$  subordinates in exactly  $\binom{\alpha}{i}$  different ways.

It follows from the above considerations that  $p_{k+1}$ , the probability that

a randomly selected neuron of the  $(k + 1)$ st stage will fire, is given by a sum of mutually exclusive probabilities, namely,

$$p_{k+1} = \sum_{i=0}^{\beta} \binom{\alpha}{i} p_k^{\alpha-i} (1 - p_k)^i. \quad (1)$$

It follows from equation (1) that  $p_{k+1}$  can be expressed as a polynomial of degree  $\alpha$  in  $p_k$ ; in fact, after elementary transformation we obtain:

$$p_{k+1} = \sum_{j=0}^{\beta} \left[ \sum_{i=j}^{\beta} \binom{i}{j} \binom{\alpha}{i} (-1)^{i+j} \right] p_k^{\alpha-j}. \quad (2)$$

Expressions (1) and (2) are iterations on  $k$ . They are, therefore, formal solutions to the problem. After  $K$  iterations we can (at least in principle) obtain  $p_K$  as a function of  $p_0$ .

Neither of these expressions, however, lends itself readily to further analysis. An alternative formulation may be obtained by the following device.

Let  $r_k$  denote the ratio of the probability of firing in the  $k$ th stage to the probability of failure. Thus

$$r_k \equiv \frac{p_k}{1 - p_k}.$$

It follows that

$$p_k = \frac{r_k}{r_k + 1}$$

and

$$1 - p_k = \frac{1}{r_k + 1}.$$

The definition of  $r_k$ , together with equation (1), implies that

$$p_{k+1} = \sum_{i=0}^{\beta} \binom{\alpha}{i} \frac{r_k^{\alpha-i}}{(r_k + 1)^{\alpha-i}} \frac{1}{(r_k + 1)^i}. \quad (3)$$

Now consider the following definitions:

$$N(r_k, \alpha) \equiv (r_k + 1)^\alpha,$$

$$F(r_k, \alpha, \beta) \equiv \text{the first } \beta + 1 \text{ terms of } N,$$

$$R(r_k, \alpha, \beta) \equiv \text{the last } \alpha - \beta \text{ terms of } N.$$

It follows from the above definitions that  $N = F + R$ . This permits us to write expression (3) in a more convenient form, namely,

$$p_{k+1} = \frac{F(r_k, \alpha, \beta)}{N(r_k, \alpha)}. \quad (4)$$

Furthermore, since

$$r_{k+1} = \frac{p_{k+1}}{1 - p_{k+1}},$$

we obtain  $r_{k+1}$  as a function of  $r_k$ , namely,

$$r_{k+1} = \frac{F/N}{1 - F/N}, \quad (5)$$

from which we find:

$$r_{k+1} = \frac{F(r_k, a, \beta)}{R(r_k, a, \beta)}. \quad (6)$$

Before proceeding it is interesting to note that equations (4) and (6) can be interpreted to represent a "pyramidal" election system.

Let us suppose that a population must decide in favor of or against a certain issue, and that they choose to render this decision by means of a ballot.

They could of course choose to settle the issue by a simple majority vote. This, however, is only one of many possible methods. The population could, for example, divide itself into many groups, each group electing an official by popular ballot within the group. The officials so elected could then decide the issue by popular ballot among themselves, or break up into smaller groups, thus carrying the process a step further. The electoral college of the United States (at least technically speaking) represents such a group of elected "electors." This procedure is carried much further in the Soviet Union.

If such an election were to take place and the official ultimately elected was given the job of deciding the issue at hand, and if, furthermore, all of the intermediate officers were completely honest with their constituents, then expressions (4) and (6) could be used to predict the outcome of the election.

In such an election the ratio  $\frac{a - \beta}{a}$  would be a measure of the required majority. Dishonesty in an elected official would be equivalent in the language of neurons to the failure to fire in spite of adequate stimulation.

Expression (4) can be easily modified to account for the case of "failure to fire in spite of adequate stimulation." Unfortunately, however, the complexity of the resulting expression makes it very difficult to use. Its form appears below:

$$p_{k+1} = \sum_{i=0}^{\beta} \sum_{j=0}^{\beta-i} \binom{a}{i} \binom{a-i}{j} C^j (1-C)^{a-i-j} p_k^{a-i} (1-p_k)^i, \quad (7)$$

where  $C$  is defined as the probability that an adequately stimulated element will nevertheless fail to fire.

The use of election terminology suggests a simple check on equation (4). Suppose that there are two candidates for an office in the  $(k+1)$ st stage, and that each of the constituents of stage  $k$  are equally disposed to vote for either of them. This means that  $p_k = \frac{1}{2}$ , whence

$$r_k = \frac{p_k}{1 - p_k} = 1.$$

Now, for simplicity, let  $\alpha = 2\beta$ , that is, an election ratio

$$\frac{\alpha - \beta}{\alpha} = \frac{1}{2}$$

is required for election. (Actually both candidates can win.) It seems intuitively evident that under these circumstances the probability  $p_{k+1}$  (that a given candidate will be elected) should be exactly one-half.

From the definition of  $N(r_k, \alpha)$ , we have  $N = (1 + 1)^\alpha$  for  $r_k = 1$ . Also,  $F(1, 2\beta, \beta)$  is simply the first half of  $N$ . Therefore,  $p_{k+1} = F/N = \frac{1}{2}$ , as we expected.

In the foregoing example we found that if  $p_k = \frac{1}{2}$ , then  $p_{k+1}$  is also one-half, regardless of the size of the population. We should expect, however, that if the population is biased (that is, if  $p_k$  is greater or less than  $\frac{1}{2}$ ),  $p_{k+1}$  will be more strongly biased in the same direction as  $p_k$ . The exaggeration of the bias in  $p_k$  expressed by  $p_{k+1}$  should depend upon the size of the population. (For the trivial case of  $\alpha = 1$ , we will always have  $p_{k+1} = p_k$  regardless of bias.)

To see how the size of the population affects an exaggeration in the bias of  $p_k$  we can look at equation (6). Let us suppose that  $p_k > \frac{1}{2}$  and, for simplicity, let  $\alpha = 2\beta$ . This implies that  $r_k > 1$ . By definition

$$R = \sum_{i=\beta+1}^{\alpha} \binom{\alpha}{i} r_k^{\alpha-i}.$$

From the symmetry of the binomial coefficients we can rewrite this expression to read

$$R = \sum_{i=0}^{\beta} \binom{\alpha}{i} r_k^i.$$

But also

$$F = \sum_{i=0}^{\beta} \binom{\alpha}{i} r_k^{\alpha-i} \quad \text{and} \quad r_{k+1} = \frac{F}{R}.$$

It follows from the foregoing that for every term  $\binom{a}{i} r_k^{a-i}$  in the numerator of  $r_{k+1}$  there is a corresponding term in the denominator, namely,  $\binom{a}{i} r_k^i$ . Now since  $r_k > 1$ , the powers of  $r_k$  will be even larger. But since  $a - i > i$ , the "exaggeration" of  $r_k$  will be greater in the terms of the numerator than those of the denominator. This effect will be increased as  $a$  is increased. Thus the larger the population, the larger will be the exaggeration of  $p_k$ .

In the above example we assumed that  $\beta = \frac{1}{2}a$ . This, of course, need not be true in general. An increase in  $\beta$  would be the same as lowering the threshold  $a - \beta$ , or the *election ratio*  $\frac{a - \beta}{a}$ .

If we let  $\frac{\Delta p_{k+1}}{\Delta \beta}$  represent the ratio of the change in  $p_{k+1}$  as  $\beta$  goes from  $\beta - 1$  to  $\beta$ , then we have

$$\frac{\Delta p_{k+1}}{\Delta \beta} = \frac{\binom{a}{\beta} r_k^{a-\beta}}{R}. \quad (8)$$

Note that for  $r_k \gg 1$ , that is,  $p_k \sim 1$ , the denominator of expression (8) is very large compared to the numerator, so that

$$\frac{\Delta p_{k+1}}{\Delta \beta}$$

approaches zero. Similarly, as  $r_k \rightarrow 0$ , that is, as  $p_k \rightarrow 0$ , the denominator approaches unity and the numerator approaches zero. The ratio

$$\frac{\Delta p_{k+1}}{\Delta \beta}$$

appears then to be most sensitive in the region of  $r_k \sim 1$  or  $p_k \sim \frac{1}{2}$ .

In order to examine more closely the behavior of  $p_{k+1}$  as a function of  $p_k$ ,  $a$ , and  $\beta$ , we can write expression (1) as the ratio of two integrals, namely,

$$p_{k+1} = \frac{\int_0^{p_k} x^{a-\beta-1} (1-x)^\beta dx}{\int_0^1 x^{a-\beta-1} (1-x)^\beta dx}. \quad (9)$$

The identity of expressions (1) and (9) can be readily proved by differentiating both expressions with respect to  $p_k$  and comparing the derivatives.

Note that the denominator ( $D^{-1}$ ) of expression (9) is the beta-function of  $\alpha - \beta$  and  $\beta + 1$ , that is to say,

$$D^{-1} = B(\alpha - \beta, \beta + 1), \quad (10)$$

where

$$B(m, n) \equiv \int_0^1 x^{m-1} (1-x)^{n-1} dx.$$

In general, however,

$$B(m, n) = \frac{\Gamma(m) \Gamma(n)}{\Gamma(m+n)}, \quad (11)$$

where  $\Gamma$  represents the well-known gamma-function. It follows then that

$$D^{-1} = \frac{\Gamma(\alpha - \beta) \Gamma(\beta + 1)}{\Gamma(\alpha + 1)}. \quad (12)$$

However, for integral  $n$ ,  $\Gamma(n) = (n-1)!$ ; hence

$$D^{-1} = \frac{(\alpha - \beta - 1)! \beta!}{\alpha!}. \quad (13)$$

But since

$$\binom{\alpha}{\beta} \equiv \frac{\alpha!}{(\alpha - \beta)! \beta!},$$

we have

$$(\alpha - \beta)^{-1} D = \binom{\alpha}{\beta},$$

so that

$$p_{k+1} = (\alpha - \beta) \binom{\alpha}{\beta} \int_0^{p_k} x^{\alpha-\beta-1} (1-x)^\beta dx. \quad (14)$$

In order to examine a particular case, let us suppose that  $\alpha = 2\beta$  and that  $\beta$  is sufficiently large to permit an approximation of  $\beta!$  by Stirling's formula. For these conditions we have

$$D = \sqrt{\frac{\beta}{\pi}} 4^\beta;$$

hence

$$p_{k+1} = \sqrt{\frac{\beta}{\pi}} 4^\beta \int_0^{p_k} x^{\beta-1} (1-x)^\beta dx. \quad (15)$$

By direct integration of expression (15) we obtain

$$p_{k+1} = \sqrt{\frac{\beta}{\pi}} 4^\beta \sum_{i=0}^{\beta-1} \frac{(-1)^i \binom{\beta}{i}}{(\beta-i)} p_k^{\beta-i}. \quad (16)$$

Note that for  $p_k$  sufficiently close to zero the first term of the polynomial in expression (16) becomes dominant so that, roughly,

$$p_{k+1} = \frac{4^\beta}{\sqrt{\pi\beta}} p_k^\beta = A p_k^\beta. \quad (17)$$

Expression (17) is a good approximation only if  $\beta p_k$  is small compared to one. A few values are listed in Table I with  $\beta$  taken equal to ten.

TABLE I

$p_k$	1/1000	1/100	1/90	1/80	1/70
$p_{k+1}$	$2.3 \times 10^{-25}$	$2.3 \times 10^{-15}$	$6.6 \times 10^{-15}$	$2.3 \times 10^{-14}$	$8.2 \times 10^{-14}$

If  $p_k$  is sufficiently small to permit the use of expression (17) then we note that  $p_{k+1}$  is very much smaller, so that we would be more justified to use equation (17) for successive iterations; hence for  $p_0$  sufficiently small we have

$$\begin{aligned}
 p_1 &= A p_0^\beta \\
 p_2 &= A^{\beta+1} p_0^{2\beta} \\
 &\vdots \\
 p_i &= A^{\beta^{i-1} + \beta^{i-2} + \dots + 1} p_0^{i\beta}.
 \end{aligned}$$

Now, if  $K$  is the number of stages in the hierarchy, then since

$$\beta^{K-1} + \beta^{K-2} + \dots + 1 = \frac{\beta^K - 1}{\beta - 1},$$

we have

$$p_K = A^{(\beta^K - 1)/(\beta - 1)} p_0^{K\beta}. \quad (18)$$

For large  $\beta$  we have

$$\frac{\beta^K - 1}{\beta - 1} \sim \frac{\beta^K}{\beta - 1},$$

so that expression (18) is approximated by

$$p_K = A^{(\beta^K/\beta - 1)} p_0^{K\beta} = \left[ \frac{4\beta}{\sqrt{\pi\beta}} \right]^{(\beta^K/\beta - 1)} p_0^{K\beta}. \quad (19)$$

On the other hand, if instead of a pyramidal ballot a direct majority vote were taken, the probability  $p_K^*$  corresponding to  $p_K$  would have a very different form. In fact

$$p_K^* = \left[ \frac{4^{(2\beta)^{K/2}}}{\sqrt{\pi} \frac{(2\beta)^K}{2}} \right]^{[(2\beta)^{K^2/2K}]/[(2\beta)^{K/2}] - 1} p_0^{K[(2\beta)^{K/2}]}. \quad (20)$$

It is rather difficult to compare expressions (19) and (20) for arbitrary  $\beta$  and  $K$ .

On the basis of a few examples, one of which is given below, it would seem that, in general,  $p_K^* < p_K$ .

For the cases  $\alpha = 4$ ,  $\beta = 2$ , and  $K = 2$  we have

$$p_K \approx \frac{6528}{6561} \quad \text{and} \quad p_K^* \approx \frac{4069}{4304}.$$

This and other special cases indicate that the hierarchy strongly suppresses the minority voice.

This analysis is, of course, not nearly general enough to constitute an adequate criticism of actual election systems. Many other factors, which have not been considered here, enter into the real situation.

It would be desirable to say something about  $p_{k+1}$  as a function of  $p_k$  for the region  $p_k \sim \frac{1}{2}$ .

Let us assume that the function  $p_k = p(k)$  can be approximated by a smooth curve continuous in  $k$  and having a continuous first derivative with respect to  $k$ . In such a case we could differentiate expression (14) and obtain

$$\left. \frac{\partial p(k)}{\partial k} \right|_{k=i+1} = (\alpha - \beta) \binom{\alpha}{\beta} [p(k)^{\alpha-\beta-1} (1 - p(k))^\beta] \left. \frac{\partial p(k)}{\partial k} \right|_{k=i}. \quad (21)$$

Equation (21) is a nonlinear differential difference equation, so that direct solution is difficult. It does, however, tell us something about the behavior of  $p(k)$ .

To begin with, notice that for the trivial cases of  $p(k) \sim 0$  and  $p(k) \sim 1$

$$\frac{\partial p(k)}{\partial k}$$

is small, as we would expect. We know from our discussion of "bias" that for  $p(k) = \frac{1}{2}$

$$\frac{\partial p(k)}{\partial k} = 0.$$

This condition is consistent with equation (21). We also know that if  $p(k)$  differs slightly from  $\frac{1}{2}$  (and  $\alpha = 2\beta$ ) that this bias will be exaggerated. In fact, roughly,

$$\left. \frac{\partial p(k)}{\partial k} \right|_{k=i+1} = \sqrt{\frac{\beta}{\pi}} 4^\beta \left(\frac{1}{2}\right)^{2\beta-1} \left. \frac{\partial p(k)}{\partial k} \right|_{k=i};$$

hence

$$\left. \frac{\partial p(k)}{\partial k} \right|_{k=i+1} = 2 \sqrt{\frac{\beta}{\pi}} \left. \frac{\partial p(k)}{\partial k} \right|_{k=i}. \quad (22)$$

Equation (22) tells us that the slope of the curve  $p_k = p(k)$  rises very rapidly with increasing  $k$ , the rate of this rise being proportional to the square root of  $\beta$ .

Further development of this theory should include the possibility that elected officers will not always follow the dictates of their constituents.

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## AN EXACT METHOD FOR THE COMPUTATION OF THE CONNECTIVITY OF RANDOM NETS

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The problem of finding the "weak connectivity" of a random net is reduced to one involving a Markov process. This provides a mathematically exact treatment of the problem which had previously been treated by an approximation, whose justification was not rigorous. The exact method allows in principle not only the calculation of the "weak connectivity," but also of the "strong connectivity," and, in general, the probability that from a randomly selected neuron in the net there exist paths to a specified number of neurons. The computations become exceedingly involved for large nets.

A previous paper (Solomonoff and Rapoport, 1951) dealt with an approximate method for determining the "weak connectivity" of random nets. The reader is referred to that paper for the definitions of terms and the statement of the problem.

In this paper we will indicate a mathematically exact method for calculating the probability that from an arbitrarily selected neuron in a random net paths exist to any specified number of neurons. The expected number of such neurons is then the "weak connectivity." On the other hand, if the specified number is the largest possible, the associated probability is the "strong connectivity."

We follow the "tracing procedure" described in the previous paper. Let  $x(t)$  represent the actual number of neurons contacted in all by the  $t$ th tracing inclusive, and let  $y(t)$  be the number of neurons *newly* contacted by the  $t$ th tracing. Then

$$x(t) = \sum_{i=0}^t y(i). \quad (1)$$

Let  $p(x, t)$  be the probability that there were  $x$  neurons in all contacted by the  $t$ th tracing. Then  $p(x, t)$  depends not only upon the possible values of  $x$  on the  $(t - 1)$ th tracing, but also upon those values on the  $(t - 2)$ th

tracing, since only the newly contacted neurons of the  $(t - 1)$ th tracing are traced on the  $t$ th. If  $x(t - 1) = i$  and  $x(t - 2) = j$ , then

$$p(x, t) = r_{x-i}[a(i - j), i]. \quad (2)$$

Here  $r_k(s, m)$  is the probability that  $k$  neurons will be newly contacted, when there are  $s$  axones being traced and there have been  $m$  neurons already contacted. The equation

$$r_k(s, m) = \binom{N-m}{k} N^{-s} \sum_{j=0}^k \binom{k}{j} (m + k - j)^s \quad (3)$$

was derived by A. Rapoport (1951). This can be more compactly written in the notation of finite differences as

$$r_k(s, m) = \binom{N-m}{k} \frac{\Delta^k(m^s)}{N^s}, \quad (4)$$

where  $\Delta^k(m^s)$  is given by the following iteration formula:

$$\begin{aligned} \Delta(m^s) &= (m + 1)^s - m^s, \\ \Delta^k(m^s) &= \Delta^{k-1}[(m + 1)^s] - \Delta^{k-1}[m^s]. \end{aligned} \quad (5)$$

Consider now an abstract system with  $N^2 + 1$  possible states. We can designate each state by an ordered pair  $(i, j)$ , where  $i$  and  $j$  range independently from 1 to  $N$ , and an additional (initial) pair  $(0, 1)$ . Furthermore, suppose that if the system is in state  $(i, j)$  at time  $t$ , then the probability that it will be in state  $(k, l)$  at time  $t + 1$  is independent of  $t$  and equals  $p[(i, j), (k, l)]$ . Hence if we designate by  $D[(i, j), t]$  the probability density distribution over all the possible states at time  $t$ , this distribution at time  $t + 1$  will be given by

$$D[(k, l), t + 1] = \sum_{(i, j)} p[(i, j), (k, l)] D[(i, j), t]. \quad (6)$$

This equation is obtained by summing over all possible ways in which the system can make transitions from states  $(i, j)$  to a state  $(k, l)$ . The  $p$ 's are, of course, the transition probabilities. The  $D$ 's are probability density distributions of the  $N^2 + 1$  possible states. We shall refer to the  $D$ 's simply as the distribution vectors.

It is now clear that we are dealing with a process which can be described in terms of a vector-matrix equation, in fact, a Markov process. The vectors have  $N^2 + 1$  components and the matrices  $N^4 + 2N^2 + 1$  com-

ponents. If we designate our transition matrix by  $P$ , equation (6) can be immediately generalized to

$$D[t+n] = P^n D(t). \quad (7)$$

This follows by a simple induction on  $n$ .

In terms of our problem we then have the following interpretation. Let  $i(t)$  be the total number of neurons contacted by the  $(t-1)$ th tracing and  $j(t)$  the total number contacted by the  $t$ th tracing. Then  $p[(i, j), (k, l)]$  is the probability of the following combination of events:

1. At  $t-1$ , there were  $i$  neurons contacted in all.
2. At  $t$ , there were  $j$  neurons contacted in all.
3. At  $t$ , there were  $k$  neurons contacted in all.
4. At  $t+1$ , there will be  $l$  neurons contacted in all.

Evidently 2. and 3. are either identical or incompatible. They were stated separately only to give meaning to the quadruple index  $(i, j, k, l)$  in terms of which the vector-matrix formulation was obtained. In view of the meaning of our indices, we see that  $p[(i, j), (k, l)] = 0$  unless  $i \leq j = k \leq l$ , so that our transition matrix  $P$  has non-zero elements at most at those loci  $[(i, j), (j, l)]$ , where  $i \leq j \leq l$ .

Now let an initial condition be known, e.g., at  $t=1$  exactly one neuron is contacted. Then the initial distribution vector is  $(1, 0, 0 \dots)$  with the unity representing the certainty of the initial state  $(0, 1)$  at  $t=1$ . The elements of the transition matrix are given by

$$p[(i, j), (j, l)] = \binom{N-j}{l-j} \frac{\Delta^{(l-j)} [j^{a(j-i)}]}{N^{a(j-i)}}. \quad (8)$$

This is essentially the expression (4) with

$k = l - j$ , the number of newly-contacted neurons at  $t+1$ ;

$m = j$ , the number of neurons in all contacted at  $t$ ;

$s = a(j-i)$ , the number of axones to be traced at  $t$ .

To find the final distribution vector at  $t = n+1$ , we multiply the initial distribution vector  $(1, 0 \dots)$  by the  $n$ th power of the transition matrix. Note that if on any tracing no new neurons are contacted, there will be no axones to trace on any subsequent tracing, and, therefore, the total number of neurons contacted will remain stationary. But there are exactly  $N-1$  uncontacted neurons at  $t=1$ . Hence there can be at most

$N - 1$  tracings, and we can set  $n = N - 1$ . The distribution vectors will remain unchanged for  $t > N$ .

Another way of looking at it is by noting that for  $t = N$ , the distribution vector is the sum of eigenvectors, each of eigenvalue unity. All the components of these eigenvectors vanish, except one of the  $(i, i)$  components. There are exactly  $N$  such eigenvectors, one for each  $i$ .

It appears, therefore, that the final distribution vector  $D[(i, j), N]$  will have non-zero components only where  $i = j$ . Each of these components with index  $(i, i)$  will represent the probability that there exist paths from an arbitrary neuron to exactly  $i$  other neurons. In particular, the component  $(N, N)$  is the "strong connectivity" of the net, which, as will be recalled, was defined in the previous paper as the probability that paths exist from an arbitrary neuron to *all* the other neurons of the net.

To find the weak connectivity  $\gamma$ , we take the expected value of  $x/N$  at  $t = N$ , so that

$$\gamma = \frac{1}{N} \sum_i i D[(i, i), N]. \quad (9)$$

In the following numerical example  $N = 4$ ,  $a = 2$ . Our transition matrix, computed from (4), is shown in Table I.

TABLE I

	0.1	1.1	1.2	1.3	1.4	2.1	2.2	2.3	2.4	3.1	3.2	3.3	3.4	4.1	4.2	4.3	4.4
0.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1.1	1/16	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1.2	9/16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1.3	6/16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2.2	0	0	2/8	0	0	0	1	0	0	0	0	0	0	0	0	0	0
2.3	0	0	5/8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2.4	0	0	1/8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3.3	0	0	0	81/256	0	0	0	9/16	0	0	0	1	0	0	0	0	0
3.4	0	0	0	175/256	0	0	0	7/16	0	0	0	0	0	0	0	0	0
4.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.4	0	0	0	0	1	0	0	0	1	0	0	0	1	0	0	0	1

The initial distribution vector of 17 components is  $(1, 0, 0 \dots)$ . At  $t = 4$  the (final) distribution vector is

$$D(4) = (0, .0625, 0, \dots .1407, \dots .316, \dots .481). \quad (10)$$

The non-zero components of this vector give the probabilities that there exist paths from an arbitrary neuron to 1, 2, 3, and 4 neurons respectively. In particular, the last value, .481, is the strong connectivity of the random net with total population 4 and axone density 2.

The weak connectivity is

$$\frac{1}{4} (1 \times .0625 + 2 \times .1407 + 3 \times .316 + 4 \times .481) = .804. \quad (11)$$

The value of  $\gamma$  given by the approximate equation (cf. Solomonoff and Rapoport, *loc. cit.*),

$$\gamma = 1 - e^{-a\gamma}, \quad (12)$$

turns out to be 0.8, a good approximation for this case.

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## CONTRIBUTION TO THE MATHEMATICAL THEORY OF MASS BEHAVIOR: I. THE PROPAGATION OF SINGLE ACTS

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The propagation of a single act in a large population is supposed to depend on some external circumstance and on an "imitation component," where encounters with individuals who are performing or have already performed the act contribute to the tendency of an individual to perform it. The "tendency" to perform is supposed to be measured by the average frequency of stimuli, randomly distributed in time, impinging on the individual. The deduced equation is a relation between the fraction of the population who have performed the act and time, provided the time course of the "external circumstance" and the way in which the imitation component contributes are known. Several special cases are studied, in particular, cases without the imitation component, cases with imitation only, and various mixed cases. Examples are given of social situations in which such factors may operate and general suggestions are made for the systematization of observations and/or experiments to test the assumptions of the theory.

By a single act, we shall understand one which is performed at most once in the lifetime of an individual or, more generally, at most once during the interval of time under consideration. Examples are suicide; marriage; conversion to a faith; or buying an item of lasting use, such as a car, a house, etc. We are going to consider the propagation of single acts throughout a large but finite population.

We shall suppose that two major influences contribute to the probability that a randomly selected individual will perform the act at a randomly selected instant of time, namely, 1) the pressure of external circumstances, and 2) the social imitation component. N. Rashevsky (1951) and H. G. Landau (1950) postulate for each individual a characteristic inherent tendency to perform an act. In their treatments the act is not generally a single act, inasmuch as it can be performed any number of times. The inherent tendency, moreover, is characteristic of the individual rather than of the external circumstances. Rashevsky and Landau suppose that to

this tendency a social imitation component is added, which depends on the number of individuals performing the act. Thus in their treatments the inherent tendency is usually independent of time, and the social imitation component only implicitly a function of time. In our treatment, however, the external influence, being independent of the individuals, will, in general, be an explicit function of time (a constant in special cases), while the imitation component will depend on the number of individuals who are performing or have performed the act (exactly once). The individuals who have performed the act will be called conforming individuals.

To take a concrete example, consider the motorists driving along a well-traveled highway at sunset. The tendency to turn on one's headlights primarily depends on the degree of darkness, which, in this case, is a monotone increasing function of time. There is, besides, another component contributing to this tendency, namely, the frequency with which one meets cars with their headlights already turned on. This is the social imitation component. Another example is a panic, revolution, or riot. The external circumstance may be a progressively unbearable environment. The social imitation component may exert its influence through the number of individuals already exhibiting the behavior in question. In special cases, the external circumstance may be an instantaneous stimulus, such as the cry "Fire!" in a theater, or a single shot precipitating a stampede of cattle.

The theoretical importance of the single act in mass behavior may well lie in the ease with which the deduced equations may be tested. Statistics on suicides, marriages, joining unions, etc., are readily available. In special cases, such as our traffic example, data may be obtained under a variety of rather well-defined conditions and even experimental controls can be introduced.

It is intuitively almost evident that the ways in which the various single acts will be propagated will show significant similarities and differences. From the standpoint of theoretical social psychology, it would be interesting to determine whether these similarities and differences correspond to those predicted by the theory. For example, the social imitation component imposes a certain modification on the imitation-free curve. It would be interesting to compare actual curves taken, respectively, from situations where imitation is or is not expected to occur, and thus test the theory. For example, the increase of turned-on lights in houses at the onset of darkness is probably independent of imitation—one does not look to see whether the neighbors have their lights on. It would be inter-

esting to see if the "turned-on headlights' " curve (for which the operation of the imitation component is assumed) departs as predicted from the "turned-on house lights' " curve. The death curve of an age group should also be imitation-free, while the suicide curve may possibly show imitation effects. If one finds an imitation effect in the traffic case, one could inquire whether such an effect is reduced or disappears entirely on a one-way road, etc., etc.

Another basis of verification may be found in comparing situations where the imitation depends on the number of individuals who have already performed the act (the number of conforming individuals) with those situations where imitation depends on the number of individuals actually performing the act (rate of conformance). Our traffic example illustrates the former, while suicides (or runs on banks) may illustrate the latter. There may be mixed cases, such as marriage, where the tendency to marry may depend both on the number of one's married friends and on the frequency with which one hears of people getting married.

Our approach to the problem will be similar to that recently developed in the probabilistic theory of neural nets (Rapoport, 1950).

As in that theory, the intensity of a gross stimulus will be described in terms of an average frequency of randomly distributed instantaneous events. The "most random" distribution of events along a time axis is the Poisson distribution, in which the events are entirely independent, i.e., the fact that a certain point on the time axis is occupied by an event has no bearing on the probability density distribution of the time of the next event.

We shall assume that the events associated with the tendency to perform an act are Poisson-distributed. A change in the intensity of the tendency means a change in the *average* frequency of the events, while the random character of the events is preserved.

Let this frequency be denoted by  $x = x(t)$ . Suppose that the threshold of activity is one, i.e., the impingement of a single event results in the performance of the act. We seek the probability distribution of the times when the act will be performed. That is to say, in a large population, all subjected to a firing frequency  $x(t)$ , we wish to determine the fraction of the population which will be performing the act in a given short interval of time  $(t, t + dt)$ .

For the act to be performed in this interval, it is necessary and sufficient that the act has not been performed at any instant prior to  $t$  and performed at  $t$ . Divide the interval  $(0, t)$  into  $n$  small sub-intervals, each

of length  $\Delta t$ , denoted by their end points  $t_1, t_2, \dots, t_n = t$ . If the stimuli are Poisson-distributed, the occurrence of a stimulus in any sub-interval does not influence the probability of its occurrence in any other sub-interval. Consequently, the probabilities of non-occurrence are also independent. Hence we may take the product of the probabilities,

$$\left\{ \prod_{i=1}^n [1 - x(t_i) \Delta t] \right\} x(t) dt = P(t) dt, \quad (1)$$

as the probability that no stimulus has occurred at any instant prior to  $t$  and that a stimulus has occurred at  $t$ . Dividing both sides of (1) by  $dt$ , and taking logarithms of both sides, we have

$$\log P(t) = \log x(t) + \sum_{i=1}^n \log [1 - x(t_i) \Delta t]. \quad (2)$$

Taking  $\Delta t$  sufficiently small to justify the approximation

$$\log [1 - x(t_i) \Delta t] \sim -x(t_i) \Delta t \quad (3)$$

and the passage from finite sum to integral, we obtain

$$\log \left[ \frac{P(t)}{x(t)} \right] = \int_0^t -x(\tau) d\tau, \quad (4)$$

whence

$$P(t) = x(t) e^{-\int_0^t x(\tau) d\tau}. \quad (5)$$

The fraction of the population who have conformed at time  $t$  will then be

$$f(t) = \int_0^t P(\tau) d\tau = \int_0^t x(\tau) e^{-\int_0^\tau x(\tau') d\tau'} d\tau. \quad (6)$$

Therefore

$$f = 1 - e^{-\int_0^t x(\tau) d\tau}. \quad (7)$$

Regarding  $P(t)$  as  $f'(t)$ , we see that equation (6) can be written as a differential equation

$$df = (1 - f) x(t) dt, \quad (8)$$

which is simply a reflection of the fact that the probability that an individual picked at random at time  $t$  is performing the act is the product of the probabilities that 1) he has not yet performed the act, and 2) that the stimulus for performing the act is at that instant impinging on him. Differential equation (8) with the initial condition  $f(0) = 0$  leads, of course, to the solution (7).

For the special case where  $x$  is independent of time, the propagation of the act is given by

$$f = 1 - e^{-xt}, \quad (9)$$

which is identical with the equations of radioactive decay, monomolecular reactions, etc. Generalizations can now be made in several directions, e.g., by introducing a threshold greater than unity, by making  $x$  variable with time, by introducing the imitation component, and by combinations of these. We shall first consider the introduction of a nontrivial threshold, while  $x$  is independent of time.

*Case 1:  $x = \text{constant}$ .* The introduction of a nontrivial threshold means that the stimuli, whose frequency measures the tendency to perform the act, must sum in order to effect an actual performance. Mathematically the situation is equivalent to that in which a single neuron with a period of latent summation  $\sigma$  and a threshold  $h$  responds to randomly distributed stimuli, when  $h$  or more of them happen to fire within  $\sigma$ . This case, including a postulated refractory period, was treated in an earlier paper (Rapport, 1951). In our present case, the individual takes the place of the neuron. The "stimuli" he receives which predispose him to perform the act may be very complicated neural processes, but for the purposes of this paper, they will be treated as Poisson-distributed instantaneous events. The meaning of the threshold  $h$  and of the period of latent summation  $\sigma$  is then quite analogous to that pertaining to the single neuron. Refractoriness, however, is meaningless, inasmuch as only one response is considered.

Since in the special case under consideration  $x$  is a constant, equation (15) of the above-mentioned paper holds, namely,

$$g(x, \sigma) = 1 - E_{h-2}(x\sigma) e^{-x\sigma}, \quad (10)$$

where  $g(x, \sigma)$  is the probability of finding at least  $h - 1$  stimuli impinging within  $\sigma$  units of time prior to an arbitrarily selected moment and  $E_k(z)$  is defined as

$$E_k(z) \equiv \sum_{j=0}^k \frac{z^j}{j!}. \quad (11)$$

Our equation (8) for general  $h$ , but constant  $x$ , then becomes

$$df = (1 - f) [1 - E_{h-2}(x\sigma) e^{-x\sigma}] dt, \quad (12)$$

whose solution is

$$-\log(1 - f) = [1 - E_{h-2}(x\sigma) e^{-x\sigma}] t + \text{constant}. \quad (13)$$

Therefore, if  $f(0) = 0$ , we have

$$f = 1 - e^{[E_{h-2}(x\sigma)e^{-x\sigma}-1]t}. \quad (14)$$

Equation (14) is of the same general form as (7), except that the time constant  $x$  is replaced by the expression  $1 - E_{h-2}(x\sigma)e^{-x\sigma}$ , which is likewise constant in time. Since the fitting of an empirical curve of the type (8) allows only the gross determination of the time constant, and not the quantities  $x$  and  $\sigma$  separately, there is no way to distinguish this case from the one where  $h = 1$ .

*Case 2:  $x$  is a function of time.* If  $h = 1$ ,  $f$  is given by equation (7). If, however,  $h > 1$ ,  $g(x, \sigma)$  now becomes  $g[x(t), \sigma]$ . Because of the total randomness of the stimuli, however, equation (6) of the earlier paper still holds and now reads:

$$P(t) dt = \left[ 1 - \int_0^t P(\tau) d\tau \right] [x(t) dt] g[x(t), \sigma]. \quad (15)$$

Replacing

$$\int_0^t P(\tau) d\tau$$

by  $f(t)$ , we have the differential equation

$$df = (1 - f) [x(t)] g[x(t), \sigma] dt, \quad (16)$$

whose formal solution is

$$f = 1 - e^{-\int_0^t x(\tau) g[x(\tau), \sigma] d\tau}. \quad (17)$$

Note that we may suppose  $\sigma$  to be very small compared with  $1/x$ , and, therefore, that  $x\sigma \ll 1$  (the quantity  $x\sigma$  is dimensionless). This is a consequence of the fact that  $\sigma$  is of the order of milliseconds, if it is an actual neurological period of latent summation; while  $1/x$ , being the average interval between rather complex events, may be of the order of seconds. Hence we may consider  $x$  constant for the interval of time comparable to  $\sigma$ . In this case  $g[x(t), \sigma]$  in the neighborhood of the instant  $t$  becomes the probability of finding  $h - 1$  or more stimuli within  $\sigma$  prior to  $t$ . And this is given for a Poisson distribution as

$$\sum_{j=h-1}^{\infty} \frac{[x(t)\sigma]^j}{j!} e^{-x(t)\sigma}. \quad (18)$$

But this is precisely the expression on the right side of (10). Equation (17) now becomes

$$f = 1 - e^{-\int_0^t x(\tau) \{e^{x(t)\sigma} - E_{h-1}[x(\tau), \sigma]\} e^{-x(\tau)\sigma} d\tau}. \quad (19)$$

Here, since  $x(t)$  is not a constant,  $t$  enters nonlinearly in the exponential of (19). Furthermore, for a given  $x(t)$ , the way  $t$  enters into (19) depends on  $h$ . Suppose, for example,  $x = at$ . Let us examine the behavior of the right side of (19) for small values of  $t$ , i.e., where a series in  $[x(t)\sigma]$  is dominated by the lowest power. Then

$$e^{x(t)\sigma} - E_{h-2} [x(t)\sigma]$$

may be replaced by the lowest term of its series representation, namely,

$$\frac{x^{h-1}\sigma^{h-1}}{(h-1)!} = \frac{a^{h-1}t^{h-1}\sigma^{h-1}}{(h-1)!}. \quad (20)$$

Then the integral within the brace of (19) becomes

$$\begin{aligned} \int_0^t \frac{a^h \tau^h \sigma^{h-1}}{(h-1)!} e^{-a\tau\sigma} d\tau &= \frac{h}{\sigma} \int_0^t \frac{(a\tau\sigma)^h e^{-a\tau\sigma}}{h!} d\tau \\ &= \frac{h}{a\sigma^2} [1 - E_h(at\sigma) e^{-at\sigma}]. \end{aligned} \quad (21)$$

Substituting this expression into (19), we see that for small values of  $t$ , approximately,

$$f = 1 - e^{-(h/a\sigma^2)[1 - E_h(at\sigma) e^{-at\sigma}]}. \quad (22)$$

Again approximating

$$[1 - E_h(at\sigma) e^{-at\sigma}] e^{-at\sigma}$$

by

$$\frac{(at\sigma)^{h+1}}{h+1!},$$

expanding the exponential, and neglecting all but the lowest power of  $t$ , we have the approximation

$$f \sim \frac{(at\sigma)^{h+1}}{h!a\sigma^2} = \frac{a^h\sigma^{h-1}}{h!} t^{h+1}. \quad (23)$$

*Remark.* This approximation holds only for  $h > 1$ . If  $h = 1$ ,  $\sigma$  has no meaning, and the derivation of the function of  $g$  does not follow. We have, in fact, from equation (7), where  $h = 1$ ,

$$f \sim \frac{at^2}{2} \quad (24)$$

for small values of  $t$ , whereas equation (23) gives for  $h = 1$ ,  $f \sim at^2$ . We summarize these results in the following

THEOREM. Let the frequency of impinging external stimuli be  $x(t) = at$ , the threshold  $h$ , and the period of latent summation  $\sigma$ . Then the fraction of individuals who have performed the act at time  $t$  is given by

$$f = 1 - e^{-\int_0^t a\tau[1 - E_{h-2}(a\tau\sigma)e^{-a\tau\sigma}]d\tau}, \quad (25)$$

which for small values of  $t$  is approximated by

$$f \sim \frac{a^h \sigma^{h-1} t^{h+1}}{h!}. \quad (26)$$

*The imitation component.* Now let each encounter with a conforming individual be a stimulus. Suppose first that  $h = 1$  for all stimuli, so that either an external stimulus or the above-mentioned encounter is sufficient to induce the act. If the frequency of encounters is proportional simply to the density of individuals who have performed the act (as is the case in our traffic example), we have

$$df = (1 - f)[x(t) + bf]dt. \quad (27)$$

If  $x$  is a constant, equation (27) can be solved by separation of variables, namely,

$$\frac{df}{(1-f)(x+bf)} = dt, \quad (28)$$

which leads in a straightforward way to the solution

$$f = \frac{x[e^{(x+b)t} - 1]}{b + x e^{(x+b)t}}. \quad (29)$$

Equation (29) is seen to reduce to (9) if  $b = 0$ , as, of course, should be the case. If  $x$  is a function of  $t$ , the differential equation (29), being nonlinear, is not readily solvable. Assuming  $f$  to be a power series in  $t$ , however, we can calculate the coefficients of that power series and compare them with those where imitation does not occur. Therefore, let

$$f = \sum_{i=1}^{\infty} c_i t^i, \quad (30)$$

and  $x = at$ , as before. Then

$$\frac{df}{dt} = \sum_{i=1}^{\infty} i c_i t^{i-1}, \quad (31)$$

and we have

$$\sum_{i=1}^{\infty} i c_i t^{i-1} = \left[ 1 - \sum_{i=1}^{\infty} c_i t^i \right] [(a + b c_1)t + b c_2 t^2 + \dots]. \quad (32)$$

Equating the coefficients of like powers, we obtain

$$c_1 = 0, \quad c_2 = \frac{a}{2}, \quad c_3 = \frac{ba}{6}, \quad c_4 = \frac{-3a^2 + b^2a}{24}, \text{ etc.} \quad (33)$$

The dimension of  $a$  is  $[T]^{-2}$ ; of  $b$ ,  $[T]^{-1}$ ; and of  $c_i$ ,  $[T]^{-1}$ . Therefore

$$f = \frac{at^2}{2} + \frac{abt^3}{6} + \frac{(ab^2 - 3a^2)t^4}{24} + \dots \quad (34)$$

The curve starts out as  $at^2/2$  as in the imitation-free case, and is perturbed by a positive term  $abt^3/6$ , which is absent in the imitation-free case. The fourth power term in the imitation-free case is  $-at^4/8$ . The perturbation in the coefficient of the fourth power is, therefore,  $+ab^2/24$ , etc.

If  $h > 1$ , we can assign a "stimulus strength" to encounters with conforming individuals, i.e., suppose that such encounters are equivalent to external stimuli. We shall outline the case for constant  $x$ . We must replace  $x(t)$  by our function

$$g[x(t), \sigma, h] = 1 - E_{h-2}[x(t)\sigma] e^{-x(t)\sigma},$$

and, evidently, if  $k < h$ ,  $bf$  must be replaced by  $g[x(t), \sigma, h - k]bf$ , since an encounter is equivalent to reducing the threshold by  $k$  units. If  $k \geq h$ ,  $bf$  remains in the equation with coefficient 1, since an encounter is alone sufficient to produce a response. Equation (27) now becomes

$$df = (1 - f) \{ g[x(t), \sigma, h] + g[x(t), \sigma, h - k]bf \} dt. \quad (35)$$

We may also mention the case of "pure imitation," where the external stimulus is negligible. Here  $x(t) = 0$ , and

$$\frac{df}{dt} = bf(1 - f). \quad (36)$$

Equation (36) is the well-known "logistic" equation, whose solution is

$$f = \frac{K e^{bt}}{1 + K e^{bt}}, \quad (37)$$

where

$$K = \frac{f(0)}{1 - f(0)}. \quad (38)$$

Obviously, if  $f(0) = 0$ , the propagation of the act will never get started. If, however, a "leadership" initiates the act, the propagation gets on the way through imitation alone, and eventually will involve every individual. Such a model may well represent the propagation of an act after an instantaneous stimulus, e.g., in a stampede or a panic.

One more class of problems will be mentioned, namely, those where the imitation factor depends on the rate of increase of conforming individuals instead of on their actual number. In actual situations, the dependence may well be on both these quantities. In the simplest case, we have by a proper modification of equation (27)

$$\frac{df}{dt} = (1-f) \left( x + b \frac{df}{dt} \right). \quad (39)$$

If  $x$  is constant, the variables are separable, and we obtain

$$df \left[ \frac{1}{1-f} - b \right] = x dt, \quad (40)$$

which leads to the solution (assuming the usual initial condition)

$$-\log(1-f) - b f = x t. \quad (41)$$

Being of mixed transcendental-algebraic type, equation (41) is not readily solvable for  $f$ , but it is for  $t$ , namely,

$$t = -\frac{1}{x} [\log(1-f) + b f]. \quad (42)$$

Since  $\log(1-f) \leq 0$ , and  $b f \geq 0$ , equation (42) has meaning only if

$$b \leq \frac{-\log(1-f)}{f} = 1 + \frac{f}{2} + \frac{f^2}{3} + \dots \quad (43)$$

for all values of  $f$  ( $0 \leq f \leq 1$ ). This is so if, and only if,

$$b \leq 1. \quad (44)$$

*Remark.* The meaning of this inequality is a consequence of our tacit assumption that imitation is propagated instantly. If  $b$  were unity under these conditions, the rate of conforming would be infinite.

Expressed as a time series in  $f$ ,  $t$  can be written as

$$t = \frac{1}{x} \left[ f(1-b) + \frac{f^2}{2} + \frac{f^3}{3} + \dots \right]. \quad (45)$$

On the other hand, for the case where imitation depends on the number of conforming individuals, we have

$$t = \frac{1}{x+b} \log \left[ \frac{x+bf}{x(1-f)} \right], \quad (46)$$

$$t = \frac{1}{x+b} \left[ \log \left( 1 + \frac{b}{x} f \right) - \log(1-f) \right], \quad (47)$$

$$t = \frac{1}{x+b} \left[ \left( \frac{b}{x} + 1 \right) f - \left( \frac{b^2}{2x^2} - \frac{1}{2} \right) f^2 + \left( \frac{b^3}{3x^3} + \frac{1}{3} \right) f^3 - \dots \right]. \quad (48)$$

Comparing the series (48) and (45), and each with the imitation-free case, we can get the perturbation of the coefficients of any number of terms desired.

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## PERIODICITIES OF OPEN LINEAR SYSTEMS WITH POSITIVE STEADY STATES

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Systems of two, three, and four linear non-homogeneous differential equations are examined with a view toward determining whether they can possibly serve as mathematical models to describe periodicities in the concentrations of substances which enhance or inhibit each other's rate of production (or dissipation). The nature of the model demands that the solutions of the differential equations be non-negative at all times, i.e., that all the steady states be positive. Conditions for periodicity and for positive steady states are derived, and it is shown that these conditions are not always compatible with each other. In particular it is shown that certain three- and four-hormone models proposed to account for the periodicities observed in the menstrual cycle cannot satisfy the above conditions for any values of the parameters and hence are inadequate.

There have been attempts to describe the periodic fluctuations of the concentrations of hormones in the blood stream associated with the menstrual cycle in terms of an open system of first-order linear differential equations, namely,

$$\frac{dx_i}{dt} = a_{i0} + \sum_{j=1}^n a_{ij}x_j \quad (i = 1, \dots, n), \quad (1)$$

where the  $x$ 's are the concentrations of the several hormones. We call such a system "open," because the constants  $a_{i0}$ , if not all zero, indicate that at least some of the concentrations  $x_i$  may be produced even in the absence of any of the substances. Hence the system exchanges matter with its environment and is in thermodynamic parlance an open system. Moreover, the substrates of the substances are all outside the system and are supposed to be inexhaustible. This, too, characterizes the system as "open."

In particular, H. Lamport (1941) examined one such system as a possible mathematical model for the "push-pull" theory of hormone interaction, where the follicle-stimulating hormone of the pituitary gland is supposed to enhance the production of estrogen, while estrogen, on the

contrary, is supposed to inhibit the production (or enhance the dissipation) of the follicle-stimulating hormone. Denoting the hormones by  $F$  and  $E$  respectively, Lampport examined the system

$$\begin{aligned}\frac{dF}{dt} &= a_{10} - a_{11}F - a_{12}E, \\ \frac{dE}{dt} &= a_{12}F - a_{22}E,\end{aligned}\tag{2}$$

where the  $a$ 's are all positive constants and the signs on the right side indicate the enhancing and inhibitory effects attributed to the hormones with the additional assumptions that each hormone dissipates at a rate proportional to its own concentration and that the pituitary is able to produce its hormone independently at the rate  $a_{10}$ , but that the ovary is unable to produce estrogen independently.

It must be noted that there are at least two ways in which one hormone may "inhibit" the rate of concentration of another. It may 1. simply enhance its dissipation (or breakdown) from the blood stream, or 2. it may act inhibitive on the cells which secrete the other hormone, that is, inhibit its rate of release into the blood stream. As long as the rate of active production (or secretion) is positive, the two types of action are formally (mathematically) equivalent. However, the inhibitive action of the second kind has no meaning once the rate of secretion has vanished. When this occurs, the intensity of inhibitive action, represented by the coefficient of the inhibiting substance on the right side of equation (1) or (2), must be set equal to zero. This abrupt change in the constants does not appear in equations (1) or (2). We must therefore assume that such equations purport to describe inhibitive action of the first kind, where in Lampport's equations the ovarian hormone is supposed to enhance the dissipation of the pituitary hormone *from the bloodstream* rather than inhibit its production or secretion by the gland. This interpretation is not in accord with the generally assumed action of ovarian hormones (cf. e.g., Grollman, 1947). We shall, however, consider equations of the type described on their own merits.

Lampport was interested in the conditions under which a system such as (2) would give rise to periodic solutions and thus would exhibit the fluctuations in the concentrations of the hormones during the menstrual cycle. A necessary condition for periodicity of the system (2) is that the equation

$$\begin{vmatrix} -a_{11} - w & a_{12} \\ a_{21} & -a_{22} - w \end{vmatrix} = 0\tag{3}$$

has a pair of pure imaginary roots. But this implies that  $a_{11} + a_{22} = 0$ , contrary to the assumption that both are positive. This contradiction, together with some numerical considerations regarding relations between the magnitude of the constants and the length of the menstrual cycle, led Lampert to conclude that a system of two linear differential equations cannot describe the periodicity of hormone concentrations in the menstrual cycle. He further concludes that this mathematical analysis makes the "push-pull" theory untenable. The latter conclusion, however, does not seem warranted. Equations (2) are not the only possible mathematical description of the "push-pull" theory. We have already pointed out that those equations do not themselves even describe the theory properly (because of the interpretation of "inhibition" inherent in them). Moreover, other types of equations could give a more adequate picture, for example, nonlinear equations or equations with more variables. It is proper, however, to examine a particular class of equations with a view of determining their possible application to phenomena such as the menstrual cycle. In this paper we undertake to examine linear open systems involving two, three, and four substances.

In 1948 R. Kesselman (unpublished) proposed three- and four-hormone models. An examination of the models revealed that the conditions for periodicity were incompatible with those for positive steady states. Kesselman's models were thus shown to be also inadequate.

These investigations led to the general question: Is it at all possible to describe the menstrual cycle periodicities of hormone concentrations in terms of a linear differential equation model under the assumptions usually made concerning the interaction of the hormones?

One would strongly suspect that linear models are, in general, inadequate. To begin with, conditions of periodicity imposed on such models imply rather stringent restrictions on the constants. We cannot expect these conditions to be *exactly* satisfied in nature. If they are only approximately satisfied, modifications of amplitude are introduced into the oscillations of concentrations either in the form of damping or reinforcement. Such effects have not been observed. On the contrary, the onset of menstruation at puberty and its termination at menopause are either abrupt or associated with irregularities not accounted for by damped oscillations. Even more serious objections to the linear model stem from the apparent ability of the cycle to restore itself following disturbances. Thus a delay of a few days in the onset of menstruation cannot be explained by a change in the constants, since such a change would affect subsequent periods as well, or perhaps disrupt them altogether.

More promise is held out by nonlinear systems such as occur, for example, in relaxation oscillations. The fluctuations in such a system are due to more or less abrupt passages from one steady state to another rather than to continuous periodic changes in concentration.

Aside from all these qualitative considerations, however, it might be worth while to settle once for all the question raised above from a purely mathematical point of view, especially in view of the fact that the answer to such a question may find applications elsewhere.

One can answer the question by deriving the necessary conditions for periodic solutions of linear systems under the restriction that the solutions (concentrations) be non-negative at all times, i.e., under the condition of positive steady states. Whenever a given system reveals an incompatibility in these conditions, it must be discarded, i.e., a model based on it must be considered inadequate. Knowledge of some such necessary conditions would enable us to discard many models in some cases on the basis of comparatively simple calculations or by inspection. Such considerations are, of course, applicable to any system purporting to describe a model where the rate of concentration of each substance is a linear function of the concentrations of all the substances in the system. Therefore, aside from the question of applicability of such systems to a theory of menstrual cycles, the problem has some general theoretical interest.

*The general case.* The most general open linear system is represented by equation (1). Henceforth we shall refer to the  $a_{i0}$  as the free constants and to the  $a_{ij}$  ( $j \neq 0$ ) as the coefficients. The general solution of such a system is in the form

$$x_i = b_i + \sum_{j=1}^n A_{ij} e^{\alpha_j t} \quad (i = 1, \dots, n), \quad (4)$$

where the  $b_i$  are the steady state values, the  $\alpha_j$  are the characteristic roots of the matrix  $(a_{ij})$ ,\* and the  $A_{ij}$  are determined by the initial conditions,  $n$  of them being constants of integration. In order for the  $x_i$  to be (ultimately) periodic and always non-negative, it is necessary and sufficient that

1. the  $b_i$  are positive;
2. there is at least one pair of pure imaginary  $\alpha$ 's;
3. the real parts of the remaining  $\alpha$ 's are all negative.

\* In all subsequent discussion the case of multiple characteristic roots of the matrix  $(a_{ij})$  will be discarded.

That the conditions are necessary can be seen from the following:

1. a vanishing or a negative  $b_i$  will imply a negative concentration at some time for some  $x_i$ ;
2. an absence of a pure imaginary pair of  $a$ 's will imply that all the solutions are sums of constants and/or transient terms (decaying exponentials) and/or terms with exponentially rising amplitudes;
3. a positive real part of some  $a$  will imply ever increasing amplitude of oscillations, hence eventual fluctuations below zero.

That the conditions are sufficient can be seen from the fact that the vanishing  $a$ 's will contribute only constants, while the negative real parts of the  $a$ 's will contribute only transient terms. If pairs of pure imaginary  $a$ 's occur, the solutions will be ultimately periodic about the (positive) steady states  $b_i$ . The arbitrary  $A$ 's can then be chosen so small that the greatest occurring minimum will still be sufficiently close to the corresponding steady state to be non-negative.

Case:  $n = 2$ . For two substances, we have in the most general case

$$\begin{aligned}\frac{dx}{dt} &= a_{10} + a_{11}x + a_{12}y, \\ \frac{dy}{dt} &= a_{20} + a_{21}x + a_{22}y.\end{aligned}\tag{5}$$

Necessary conditions for periodicity are

$$a_{11} + a_{22} = 0; \quad |a_{ij}| > 0.\tag{6}$$

The conditions for positive steady states are obtained by setting  $dx_i/dt = 0$  and solving the resulting algebraic system. The solutions are the  $b_i$  and must be positive. Hence

$$\frac{\begin{vmatrix} -a_{10} & a_{12} \\ -a_{20} & a_{22} \end{vmatrix}}{|a_{ij}|} > 0; \quad \frac{\begin{vmatrix} a_{11} - a_{10} \\ a_{21} - a_{20} \end{vmatrix}}{|a_{ij}|} > 0.\tag{7}$$

Suppose conditions (6) are satisfied. Then, whether the  $a_{ii}$  vanish or not, we can write  $a_{22} = -a_{11}$ . Moreover since  $|a_{ij}| > 0$ , inequalities (7) reduce to

$$\begin{aligned}(a_{10}a_{11} + a_{20}a_{12}) &> 0, \\ (-a_{11}a_{20} + a_{21}a_{10}) &> 0.\end{aligned}\tag{8}$$

We have proved

*Theorem 1. A linear open system has periodic solutions with positive steady states if, and only if, (6) and (8) hold.*

That (6) and (8) can be simultaneously satisfied if the free constants do not both vanish can be seen from the following example:

$$\begin{aligned}\frac{dx}{dt} &= 1 + x - y, \\ \frac{dy}{dt} &= 2x - y,\end{aligned}\tag{9}$$

which does have periodic solutions with non-negative steady states, for example,

$$\begin{aligned}x &= 1 + \sin t, \\ y &= 2 + \sin t - \cos t.\end{aligned}\tag{10}$$

In the light of *Theorem 1* we see that Lamport's model failed because it had a non-vanishing trace (as he himself pointed out). A model with a vanishing trace implies that either one of the substances is "auto-catalytic" (i.e., its rate of production is enhanced by its own concentration) or only "cross-effects" operate (the concentration of each affects only the rate of production or dissipation of the other) plus constants denoting independent rates of production or dissipation. We stress the rather obvious importance of the vanishing trace in the two-substance case, because this condition is *not* necessary in cases where  $n > 2$ . Thus, as we shall see, Kesselman's model failed for entirely different reasons.

*Case n = 3.* The equation analogous to (3) for this case can be written as

$$\omega^3 - T_1\omega^2 + T_2\omega - \Delta = 0,\tag{11}$$

where  $T_1$  is the trace of  $(a_{ij})$ , i.e., the sum of its principal minors of order one,  $T_2$  is the sum of the principal minors of order two, and  $\Delta$  (which could be written as  $T_3$ ) is the "sum" of the principal minors of order three, i.e., the determinant of  $(a_{ij})$ . Equation (11), being of odd degree, must have a real root, and by our conditions above, this root must not be positive. The other two roots must be pure imaginary conjugates. Hence the factored form of (11) must appear thus:

$$(\omega^2 + r_1^2)(\omega + r_2) \equiv \omega^3 + r_2\omega^2 + r_1^2\omega + r_1^2r_2 = 0,\tag{12}$$

where  $r_2 \geq 0$  and, of course,  $r_1^2 \geq 0$ . Equating the coefficients of (11) and (12), we obtain the conditions of periodicity:

$$T_1 \leq 0; \quad T_2 > 0; \quad \Delta \leq 0.\tag{13}$$

It will now be shown that if  $\Delta = 0$ , the case reduces to the case  $n = 2$ . Let  $\Delta_i$  be the Cramer determinants, obtained from  $\Delta$  by replacing the  $i$ th

column by the constants  $-a_{i0}$ . Then, formally solving for the steady states by Cramer's rule, we have

$$b_i = \frac{\Delta_i}{\Delta} \quad (i = 1, 2, 3). \quad (14)$$

If  $\Delta = 0$ , we must have each  $\Delta_i = 0$  for finite steady states. This, however, implies

$$\begin{aligned} a_{30} &= c_1 a_{10} + c_2 a_{20}, \\ a_{3j} &= c_1 a_{1j} + c_2 a_{2j}, \end{aligned} \quad (15)$$

and, consequently,

$$\frac{dx_3}{dt} = c_1 \frac{dx_1}{dt} + c_2 \frac{dx_2}{dt}. \quad (16)$$

Integrating (16), we obtain

$$x_3 = c_1 x_1 + c_2 x_2 + c_0. \quad (17)$$

Therefore our third substance may be considered to be composed of constant fractions of the other two, plus a constant amount  $c_0$ , which does not participate in the reactions. Renaming the substances

$$\begin{aligned} x'_1 &= x_1(1 + c_1), \\ x'_2 &= x_2(1 + c_2), \end{aligned} \quad (18)$$

we obtain a system of essentially two interacting substances and an inert third one. But this is the case treated above. Hence the only non-degenerate case for  $n = 3$  is where  $r_2 > 0$ , i.e.,

$$T_1 < 0; \quad T_2 > 0; \quad \Delta < 0. \quad (19)$$

Further examination of equations (11) and (12) shows that for periodicity we must also have

$$\Delta = T_1 T_2. \quad (20)$$

To realize positive steady states, we must have, in addition, because of equation (14), the Cramer determinants of the same sign as  $|a_{ij}|$ . Hence

$$\Delta_i < 0. \quad (21)$$

Conditions (19), (20), and (21) now constitute the necessary and sufficient conditions for periodic solutions with positive steady states of a three-substance open linear system. Obviously only very special systems will satisfy all three conditions. The interesting question, however, is whether a system subject to certain restrictions on the coefficients and the free constants can be *made* to satisfy the conditions by fixing these

parameters within the limits of the restrictions. Suppose, for example, all the free constants  $a_{i0} = 0$ . Then no value of the coefficients  $a_{ij}$  will insure positive steady states. Or suppose all but one of the free constants must vanish, and the signs of the coefficients are fixed. Then, depending on the distribution of these signs, conditions (19), (20), and (21) may or may not be compatible with respect to the system in question. It is questions such as these that we undertake to investigate here.

*Theorem 2.* *If no restrictions are placed on the free constants  $a_{i0}$ , any system which satisfies conditions (19) and (20) can be made to satisfy (21) by giving proper values to the constants  $a_{i0}$ .*

*Proof.* Setting  $dx_i/dt = 0$ , we can consider the resulting system as three equations of three planes. If  $\Delta \neq 0$ , the planes intersect at a point whose coordinates represent the three steady states. For positive steady states, this point must lie in the first octant. The direction cosines of the planes are determined only by the coefficients  $a_{ij}$ . Hence moving the planes by translation involves changes only in the constants  $a_{i0}$ . Thus by giving proper values to the  $a_{i0}$ , the planes can be so moved, without changing their direction cosines, as to place the intersection in the first octant.

*Remark.* *Theorem 2* can be immediately generalized to any number of variables.

The situation is different if restrictions are placed on the free constants. In particular, let it be required that one or two of these constants vanish. This means that the corresponding substances cannot be produced (or dissipated) independently. In our three-dimensional case, the vanishing of one  $a_{i0}$  means that one of our planes must go through the origin. If the  $a_{ij}$  are fixed, the plane is completely determined. The translation of the intersection point of the three planes must, therefore, take place within that plane. If that plane has points in the first octant, a translation of the intersection into that octant is possible; otherwise not. Now a plane through the origin has points in the first octant if, and only if, there is a change of signs among its coefficients. We thus have

*Theorem 3.* *Let  $a_{i0} = 0$ . Then conditions (19), (20), and (21) are compatible only if a change of sign occurs among the coefficients  $a_{i1}$ ,  $a_{i2}$ , and  $a_{i3}$ .*

If two of the constants  $a_{i0}$  vanish, the compatibility condition is more stringent. For in that case, our translation must take place along a line through the origin. The line goes through the first octant if, and only if, all three of its direction cosines are positive. These direction cosines are determined by the two-rowed minors of the matrix, whose elements are the coefficients of the equations which determine the line. Now conditions

(19), (20), and (21) all involve two-rowed minors of the matrix  $a_{ij}$ , hence they may be incompatible. To fix ideas, suppose our system is

$$\begin{aligned}\frac{dx}{dt} &= a_{10} + a_{11}x + a_{12}y + a_{13}z, \\ \frac{dy}{dt} &= a_{21}x + a_{22}y + a_{23}z, \\ \frac{dz}{dt} &= a_{31}x + a_{32}y + a_{33}z.\end{aligned}\tag{22}$$

For such a system, a necessary condition for the compatibility of (19), (20), and (21) is given by

*Theorem 4.* Let  $a_{20} = a_{30} = 0$ . Then for compatibility of periodicity and positive steady state conditions, it is necessary that

$$\begin{vmatrix} a_{21} & a_{22} \\ a_{31} & a_{32} \end{vmatrix} > 0; \quad \begin{vmatrix} a_{22} & a_{23} \\ a_{32} & a_{33} \end{vmatrix} > 0; \quad \begin{vmatrix} a_{23} & a_{21} \\ a_{33} & a_{31} \end{vmatrix} > 0. \tag{23}$$

*Proof.* Under the conditions of the theorem, it is easy to show that (23) is equivalent to (21).

We emphasize again that we are deriving necessary, not sufficient, conditions for compatibility. As we shall presently see, Kesselman's model satisfied conditions (19) and (21), and, being of the type considered in *Theorem 4*, it satisfied (23). Yet, as we shall show, for this model (the signs of whose coefficients were fixed by the physiological assumptions) conditions (20) and (23) are incompatible.

We are now in a position to examine Kesselman's three-hormone model. It involves the follicle-stimulating hormone, an effective resultant of the luteinizing and the luteotrophic hormones, and estrogen, denoted by  $F$ ,  $L$ , and  $E$  respectively. The equations

$$\begin{aligned}\frac{dF}{dt} &= a_{10} - a_{11}F - a_{13}E, \\ \frac{dL}{dt} &= -a_{22}L + a_{23}E, \\ \frac{dE}{dt} &= a_{31}F + a_{32}L - a_{33}E\end{aligned}\tag{24}$$

reflect the following assumptions:

1.  $F$  only can be produced independently;
2.  $E$  inhibits  $F$ ;
3.  $E$  enhances  $L$ ;

4.  $F$  and  $L$  enhance  $E$ ;

5. all substances dissipate proportionately to their respective concentrations. All  $a$ 's are positive.

The matrix  $(a_{ij})$  corresponding to the system (24) is

$$\begin{pmatrix} -a_{11} & 0 & -a_{13} \\ 0 & -a_{22} & a_{23} \\ a_{31} & a_{32} & -a_{33} \end{pmatrix}. \quad (25)$$

We see that the inequality  $T_1 < 0$  of (19) is satisfied. Conditions (23) are satisfied if

$$a_{22}a_{33} - a_{23}a_{32} > 0, \quad (26)$$

and this inequality also insures the inequalities  $T_2 > 0$  and  $\Delta < 0$  of (23). Let us, however, look at condition (20).

Expanding the determinant and the minors, we have

$$\begin{aligned} & -a_{11}(a_{22}a_{33} - a_{23}a_{32}) = \\ & - (a_{11} + a_{22} + a_{33})[a_{11}a_{22} + (a_{22}a_{33} - a_{23}a_{32}) + (a_{11}a_{33} + a_{13}a_{31})]. \end{aligned} \quad (27)$$

Simplifying (27), we obtain

$$\begin{aligned} & -a_{11}^2a_{22} - a_{11}(a_{11}a_{33} + a_{13}a_{31}) - (a_{22} + a_{33})a_{11}a_{22} \\ & - (a_{22} + a_{33})(a_{22}a_{33} - a_{23}a_{32}) - (a_{22} + a_{33})(a_{11}a_{33} + a_{13}a_{31}) = 0. \end{aligned} \quad (28)$$

But (28) contradicts (26), since if (26) holds, all of the terms of (28) are negative. Hence Kesselman's model fails.

*Remark.* In this particular case we had to examine all the conditions of compatibility. However the inadequacy of a model may sometimes become apparent earlier, since only *one* of such conditions need fail to reveal the inadequacy of the model. Suppose, for example, that estrogen inhibited instead of enhanced the luteinizing hormone. Such a situation would not *qualitatively* contradict the "push-pull" theory, because according to it the hormones of the pituitary still enhance that of the ovary, and the hormone of the ovary still has a negative back-action on the hormones of the pituitary. However under this assumption we should have in the matrix (25)  $-a_{23}$  instead of  $a_{23}$ , and inequalities (23) would be immediately violated, since the third two-rowed minor would then be

$$\begin{vmatrix} -a_{23} & 0 \\ -a_{33} & a_{31} \end{vmatrix} = -a_{23}a_{31} < 0. \quad (29)$$

We now pass to the conditions for compatibility of the four-substance model.

Case:  $n = 4$ . The condition of periodicity now becomes

$$\omega^4 - T_1\omega^3 + T_2\omega^2 - T_3\omega + \Delta = 0, \quad (30)$$

where the  $T$ 's have meanings analogous to those in the previous case. Among the roots of this equation there must be a pair of pure imaginaries, the other two roots being complex with non-positive real parts (in particular, they may be real non-positive or pure imaginary). At any rate, the factored form of (30) must be

$$\begin{aligned} &(\omega^2 + r^2)(\omega + a + b_i)(\omega + a - b_i) \\ &= \omega^4 + 2a\omega^3 + (a^2 + b^2 + r^2)\omega^2 + 2ar^2\omega + r^2(a^2 + b^2) = 0, \end{aligned} \quad (31)$$

where  $a \geq 0$ . Comparison with (30) shows that

$$T_1 \leq 0; \quad T_2 > 0; \quad T_3 \leq 0; \quad \Delta \geq 0. \quad (32)$$

Of interest is the case where  $\Delta > 0$ . The condition analogous to (20) is

$$T_1T_2T_3 = T_3^2 + \Delta T_1. \quad (33)$$

If only one of the constants  $a_{i0}$  or three of these constants vanish, the conditions for compatibility are entirely analogous to the corresponding ones for  $n = 3$ . The intermediate case, where exactly two of the free constants vanish, is more involved. Suppose  $a_{30} = a_{40} = 0$ . For a non-degenerate case, we must have at least one non-vanishing two-rowed minor in equations

$$\begin{aligned} a_{11}x_1 + a_{12}x_2 + a_{13}x_3 + a_{14}x_4 &= 0, \\ a_{21}x_1 + a_{22}x_2 + a_{23}x_3 + a_{24}x_4 &= 0. \end{aligned} \quad (34)$$

Let  $a_{11}a_{22} - a_{12}a_{21} \neq 0$ . Then the hyperplane determined by (34) must have points with all positive coordinates, i.e., equations (34) must be satisfied by some combination of positive  $x$ 's. Solving for  $x_1$  and  $x_2$  in terms of  $x_3$  and  $x_4$ , we have

$$\begin{aligned} x_1 &= -x_3 \frac{\begin{vmatrix} a_{13} & a_{12} \\ a_{23} & a_{22} \end{vmatrix}}{\begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix}} - x_4 \frac{\begin{vmatrix} a_{14} & a_{12} \\ a_{24} & a_{22} \end{vmatrix}}{\begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix}}, \\ x_2 &= -x_3 \frac{\begin{vmatrix} a_{11} & a_{13} \\ a_{21} & a_{23} \end{vmatrix}}{\begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix}} - x_4 \frac{\begin{vmatrix} a_{11} & a_{14} \\ a_{21} & a_{24} \end{vmatrix}}{\begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix}}, \end{aligned} \quad (35)$$

which can be written as

$$\begin{aligned}(a_{11}, a_{22})x_1 + (a_{13}, a_{22})x_3 + (a_{14}, a_{22})x_4 &= 0, \\ (a_{11}, a_{22})x_2 + (a_{11}, a_{23})x_3 + (a_{11}, a_{24})x_4 &= 0.\end{aligned}\quad (36)$$

Here the parentheses are obvious abbreviations for the two-rowed determinants in (35). Equations (36) can be satisfied for some choice of positive  $x$ 's only if a change in sign occurs among the coefficients of each equation in (36). If this does occur, there are eight distinct cases symbolized as sign arrangements of the terms on the left side of (36) as follows:

$$\begin{array}{llll} \text{I:} & \begin{array}{c} + + - \\ + + - \end{array} ; & \begin{array}{c} + - + \\ + - + \end{array} ; & \begin{array}{c} - + - \\ - + - \end{array} ; & \begin{array}{c} - - + \\ - - + \end{array} ; \\ & & & & \\ \text{II:} & \begin{array}{c} + + - \\ + - + \end{array} ; & \begin{array}{c} + - + \\ + + - \end{array} ; & \begin{array}{c} - + - \\ - - + \end{array} ; & \begin{array}{c} - - + \\ - + - \end{array} . \end{array}\quad (37)$$

*Cases I* can always be satisfied by a proper choice of the  $x$ 's. *Cases II* can be satisfied only if certain inequalities hold. We shall examine one such sample case, namely,

$$\begin{aligned}A_1x_1 + A_3x_3 - A_4x_4 &= 0, \\ A_2x_2 - B_3x_3 + B_4x_4 &= 0,\end{aligned}\quad (38)$$

where now the  $A$ 's and  $B$ 's are the absolute values of the coefficients in (36). Remembering that  $x_1$  and  $x_2$  may be arbitrary as long as they are positive, we write

$$\begin{aligned}A_4x_4 - A_3x_3 &> 0, \\ -B_4x_4 + B_3x_3 &> 0,\end{aligned}\quad (39)$$

whence

$$\frac{B_4x_4}{B_3} < x_3 < \frac{A_4x_4}{A_3}.\quad (40)$$

Since also  $x_4$  is arbitrary, we must have

$$\frac{B_4}{B_3} < \frac{A_4}{A_3}.\quad (41)$$

These results can be summarized in

*Theorem 5. If two free constants in the case  $n = 4$  vanish, the condition of compatibility is satisfied if a) there is a change in sign occurring among the coefficients of each equation in (36) and b) either a pair of coefficients of the same variable have the same sign or corresponding inequalities of type (41) are satisfied.*

One of the four-hormone models offered by Kesselman involves progesterone  $P$ , which enters the system in the following equation

$$\frac{dP}{dt} = a_{42}L - a_{44}P, \quad (42)$$

which states that progesterone is enhanced by the luteinizing hormone and dissipates proportionately to its own concentration. No action of progesterone on the other hormones is assumed here. Then the first three equations are independent of  $P$  and must satisfy the conditions of compatibility separately. But we have seen that they do not do so. Hence also this model fails. If it is assumed that progesterone does affect the other hormones, corresponding terms must be added to the other equations, and the resulting system tested for compatibility in accordance with the criteria developed for the case  $n = 4$ . We note that if an inhibitory action is assumed by progesterone on the luteinizing hormone, as Kesselman suggests quoting C. D. Turner (1948), and if progesterone cannot be produced independently, the conditions for positive steady states fail, as can be readily verified by examining the expanded matrix. Similar results obtain if progesterone is supposed to inhibit only the follicle-stimulating hormone or both of the pituitary hormones.

Generalizations of the foregoing discussion to cases with a greater number of variables is laborious but straightforward. This method may serve as a means of discovering incompatibilities in models proposed for cyclic phenomena based on linear open systems where restrictions (such as positive concentrations) are imposed by the nature of the case. Timely discovery of such incompatibilities may serve to save a considerable amount of labor in the attempts to test the theoretical value of the model.

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## THE EXCITATION OF THE HEART AND ITS MODIFICATION UNDER THE INFLUENCE OF THE CHEMICAL MEDIATORS AND THE CARDIAC NERVES: I. SOME GENERAL CONSEQUENCES OF THE ONE-FACTOR THEORY

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A generalized form of the one-factor theory is applied to the heart. It is found that the effects of acetylcholine and sympathin on the chronaxie can be accounted for only if the decay constant of the excitatory state increases in the presence of acetylcholine, and decreases in the presence of sympathin. With the assumption that this is the only effect of the chemical mediators, it is shown that upon application of acetylcholine to the heart the theory predicts: 1) a rise in the rheobase; 2) an increase in the time required for excitation by constant currents; 3) no change in the threshold with condenser discharges of brief duration; 4) a decrease in the spontaneous heart rate; 5) a sudden and complete inhibition of the spontaneous heart rate with excessive concentrations of acetylcholine. In general, the effects of sympathin predicted by the theory oppose those of acetylcholine.

During the last twenty years, various formal mathematical theories have been proposed and developed to account for the excitation and conduction properties of nerve fibers (see Rashevsky, 1948). Since, in many instances, the excitation processes in nerve fibers run parallel to those in cardiac muscle, it is reasonable to suppose that the same formal theories will be useful in discussions of cardiac excitation. For example, H. D. Landahl and J. B. Kahn (1948) have been able to account for the effects of subthreshold currents on nerves in terms of Rashevsky's two-factor theory. These results, together with the fact that the observed effects of subthreshold currents on nerve and heart are similar (Gilson and Peugnet, 1932), indicate that the two-factor theory may be able to account for these phenomena in the heart.

The purpose of this paper will be to develop, with a minimum number of plausible assumptions, certain qualitative features of a generalized form

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of Blair's one-factor theory, which will be applied to the heart. This particular theory has been selected because of its simplicity and because it can be regarded as a first approximation to the other theories.

If a stimulus  $S(t)$  is applied to an excitable structure, then, according to what is, perhaps, the most general form of the one-factor theory, the change in the excitatory state  $\epsilon$  of that structure will be given by

$$\frac{d\epsilon}{dt} = F[S(t)] - k\epsilon, \quad (1)$$

where  $k$  is a constant and  $F$  is some function of  $S$  and, consequently, a function of the time  $t$ . Excitation is to take place as soon as  $\epsilon$  reaches a threshold  $h$ , which is constant. When the structure is stimulated by means of an electrical current, it has been assumed that  $F(S) = KI$ , where  $I$  is the intensity of the current and  $K$  is a constant of proportionality. If a constant current is used and  $\epsilon(0) = 0$ , the following expressions for the chronaxie  $\tau$ , rheobase  $R$ , and time  $t^*$  required for excitation may be readily derived from (1) (Rashevsky, *loc. cit.*):

$$\tau = \frac{\log_e 2}{k}, \quad (2)$$

$$R = \frac{kh}{K}, \quad (3)$$

$$t^* = \frac{1}{k} \log_e \frac{I}{I-R}. \quad (4)$$

It has been demonstrated by numerous investigators (cf. Rosenblueth, 1950) that the vagus and sympathetic nerves exert their effects on the heart primarily by releasing acetylcholine and sympathin respectively with each impulse. Since the qualitative results of experiments are independent of the method of application of the mediator (i.e., local application or nerve stimulation), we will hereafter refer only to the concentration of the mediator.

It has been observed that the chronaxie of the heart will decrease upon the application of acetylcholine and increase upon the application of sympathomimetic substances (Fredericq, 1928). If we assume that equation (2) applies to the heart, then from the above empirical result it follows that  $k$  must increase upon the application of acetylcholine and decrease upon the application of sympathin. We shall assume that this is the only effect of the chemical mediators, and show that the one-factor theory qualitatively predicts the following events, each of which has been experimentally observed.

1. The rheobase  $R$  increases in the presence of acetylcholine [observed by Ashman and Garrey (1931)]. This result is predicted by equation (3).

2. The time  $t^*$  increases in the presence of acetylcholine [observed by Ashman and Garrey (loc. cit.)]. Differentiating  $t^*$  with respect to  $k$  in (4), and using (3), leads to the expression

$$\frac{\partial t^*}{\partial k} = \frac{h}{Kk(I-R)} - \frac{1}{k^2} \log_e \frac{I}{I-R}. \quad (5)$$

The relations

$$I = \frac{R}{1 - e^{-kt^*}} \quad (6)$$

and

$$\frac{1}{I-R} = \frac{1}{I} \frac{I}{(I-R)} = \frac{1}{I} e^{kt^*} \quad (7)$$

can be obtained readily from (4). Because of (4), (6), and (7), (5) can be written as

$$\frac{\partial t^*}{\partial k} = \frac{1}{k} \left[ \frac{1}{k} e^{kt^*} - \left( t^* + \frac{1}{k} \right) \right]. \quad (8)$$

Since for  $t^* = 0$

$$\left( \frac{\partial t^*}{\partial k} \right)_{t^*=0} = 0, \quad (9)$$

and for  $t^* > 0$

$$\frac{d}{dt^*} \left( \frac{1}{k} e^{kt^*} \right) > \frac{d}{dt^*} \left( t^* + \frac{1}{k} \right); \quad (10)$$

it follows that

$$\frac{\partial t^*}{\partial k} > 0,$$

and, therefore,  $t^*$  will increase in the presence of acetylcholine.

3. When excited by condenser discharges of brief duration, the threshold of the heart is not significantly altered by acetylcholine [observed by Gilson (1939)].

This finding can be accounted for as follows. For a condenser discharge,  $I$  may be written in the form

$$I = B e^{-bt}, \quad (11)$$

where  $B$  and  $b$  are constants. It will be shown that with a sufficiently large but fixed value of  $b$ , the smallest value of  $B$  that will excite is independent of  $k$ . This value of  $B$  may be obtained from the condition that the maximum value of  $\epsilon$  is  $h$ , that is, the condition that  $\epsilon = h$  and  $d\epsilon/dt = 0$

simultaneously at a time  $t = t'$ . Inserting (11) into (1), and integrating with  $\epsilon(0) = 0$ , yields

$$\epsilon = \frac{KB}{b-k} (e^{-kt} - e^{-bt}). \quad (12)$$

As  $b$  increases, the time taken by the condenser to discharge decreases, and we naturally expect the time for excitation to decrease. Therefore, if we choose  $b$  large enough so that  $b \gg k$  and  $e^{-kt'} \approx 1 - kt'$ , then, for  $t < t'$ , (12) reduces to

$$\epsilon = \frac{KB}{b} (1 - kt - e^{-bt}). \quad (13)$$

Since at  $t = t'$ ,  $d\epsilon/dt = 0$ , (13) implies

$$b e^{-bt'} = k, \quad (14)$$

or

$$t' = \frac{1}{b} \log_e \frac{b}{k}. \quad (15)$$

Inserting (15) into (13), with  $t = t'$  and  $\epsilon = h$ , we obtain the relation

$$\frac{KB}{b} \left( 1 - \frac{k}{b} - \frac{k}{b} \log_e \frac{b}{k} \right) = h. \quad (16)$$

Equation (16) may be rearranged to read

$$B = \frac{bh}{K \left( 1 - \frac{k}{b} - \frac{k}{b} \log_e \frac{b}{k} \right)}, \quad (17)$$

and, as  $b$  becomes larger,  $B$  approaches

$$B = \frac{bh}{K}, \quad (18)$$

which is independent of  $k$ .

4. *The interval between heart beats T increases upon application of acetylcholine and decreases upon application of sympathin [experimental evidence cited by Rosenbluth (loc. cit.)].* The fact that a heart beats spontaneously must be interpreted, in terms of the present theory, to mean that  $\epsilon$  is greater than zero (i.e.,  $\epsilon = h$ ) at the beginning of each excitation. It follows from equation (1) that in a spontaneously beating heart, regardless of the mechanism involved,  $F(S)$  cannot be identically zero, even when no external stimulus is applied. If, during the interval between beats,  $F[S(t)]$  is continuous and independent of the concentration of acetylcholine, then,

without any further assumptions about  $F$ , it will be shown that  $\partial T / \partial k > 0$ .

First note that the general solution to (1) may be written as

$$\epsilon(t) = \epsilon(0) e^{-kt} + e^{-kt} \int_0^t F[S(\theta)] e^{k\theta} d\theta, \quad (19)$$

where  $t = 0$  at the time of the preceding beat.

In equation (1),  $k$  refers only to the decay of  $\epsilon$ , and for this reason we will assume that  $k$  is independent of the type of stimulus involved. Therefore, the magnitude of  $k$  can be calculated from equation (2) if we know the value of  $\tau$ . The chronaxie of the dog's auricle has been measured and found to range from 2 to 5 milliseconds (Brucke, 1930). This result and equation (2) yield a magnitude of  $k$  which is of the order of 200 sec.<sup>-1</sup>. Because hearts with a period of less than 0.2 sec. are rarely encountered, the term  $\epsilon(0)e^{-kt}$  may be neglected in equation (19) at the time excitation occurs, leaving

$$\epsilon(t) = e^{-kt} \int_0^t F[S(\theta)] e^{k\theta} d\theta. \quad (20)$$

The exponential  $e^{k\theta}$  is positive everywhere, and, therefore, the mean value theorem may be applied to the integral in (13), yielding

$$\begin{aligned} \epsilon(t) &= e^{-kt} F[S(\xi_t)] \int_0^t e^{k\theta} d\theta \\ &= \frac{F[S(\xi_t)]}{k} (1 - e^{-kt}) \\ &\approx \frac{F[S(\xi_t)]}{k} \end{aligned} \quad (21)$$

where  $0 \leq \xi_t \leq t$ .

At excitation,  $t = T$ ,  $\epsilon = h$ , and (21) becomes

$$\epsilon(T) = \frac{F[S(\xi_T)]}{k} = h. \quad (22)$$

Since  $F[S(\xi_t)]$  depends on both  $t$  and  $k$ , the notation may be changed by defining

$$F[S(\xi_t)] \equiv f(t, k). \quad (23)$$

The relation obtained from (22),

$$f(T, k) - kh = 0, \quad (24)$$

implicitly defines  $T$  as a function of  $k$ , and implicit differentiation of (24) yields

$$\frac{\partial T}{\partial k} = \frac{h - \left( \frac{\partial f}{\partial k} \right)_{t=T}}{\left( \frac{\partial f}{\partial t} \right)_{t=T}}. \quad (25)$$

To prove that  $\partial T / \partial k > 0$ , it will be sufficient to show that both the numerator and the denominator on the right-hand side of (25) are positive within the range of  $T$ . With this end in mind, we may write, by a comparison of (20) and (21),

$$f(t, k) = k e^{-kt} \int_0^t F[S(\theta)] e^{k\theta} d\theta, \quad (26)$$

and, differentiating (26) with respect to  $k$ , we arrive at

$$\frac{\partial f}{\partial k} = (1 - kt) e^{-kt} \int_0^t F[S(\theta)] e^{k\theta} d\theta + k e^{-kt} \int_0^t \theta F[S(\theta)] e^{k\theta} d\theta. \quad (27)$$

Combining (20) and (22) yields

$$h = e^{-kT} \int_0^T F[S(\theta)] e^{k\theta} d\theta, \quad (28)$$

and it follows that

$$\left( \frac{\partial f}{\partial k} \right)_{t=T} = (1 - kT) h + k e^{-kT} \int_0^T \theta F[S(\theta)] e^{k\theta} d\theta. \quad (29)$$

Let us assume, for the moment, that  $F[S(\theta)] \geq 0$  for  $0 \leq \theta \leq T$ . Then, an application of the mean value theorem to the integral in (29) leads to the expression

$$\begin{aligned} \left( \frac{\partial f}{\partial k} \right)_{t=T} &= (1 - kT) h + \eta k e^{-kT} \int_0^T F[S(\theta)] e^{k\theta} d\theta \\ &= (1 - kT) h + \eta k h, \end{aligned} \quad (30)$$

where  $0 \leq \eta \leq T$ . Now  $\eta$  cannot be equal to  $T$ , for if it were, then

$$T \int_0^T F[S(\theta)] e^{k\theta} d\theta = \int_0^T \theta F[S(\theta)] e^{k\theta} d\theta, \quad (31)$$

and, differentiating both sides of (31) with respect to  $T$ ,

$$\int_0^T F[S(\theta)] e^{k\theta} d\theta + T F[S(T)] e^{kT} = T F[S(T)] e^{kT}, \quad (32)$$

or

$$\int_0^T F[S(\theta)] e^{k\theta} d\theta = 0. \quad (33)$$

But the integral in (33) cannot be zero, since according to (28) it is equal to  $he^{kT}$ . Then  $0 \leq \eta < T$ , and from (30) the numerator  $N$  in (25) is given by

$$N = h - \left( \frac{\partial f}{\partial k} \right)_{t=T} = k(T - \eta)h > 0. \quad (34)$$

Expression (34) was derived on the assumption that  $F[S(\theta)]$  was positive for  $0 \leq \theta \leq T$ . If  $F$  has negative values within this interval, the inequality  $N > 0$  holds *a fortiori*, since, according to (29), the contribution of

$$\left( \frac{\partial f}{\partial k} \right)_{t=T}$$

to (34) will be smaller.

To prove the denominator,

$$\left( \frac{\partial f}{\partial t} \right)_{t=T},$$

in (25) is greater than or equal to zero, first note that  $F[S(\theta)]$  was assumed to be a continuous function of time (for  $0 \leq \theta \leq T$ ) and hence, according to (26),  $f(t, k)$  is a continuous function of time. Thus it is permissible to expand  $f(t, k)$  about the point  $T$  and arrive at

$$f(T - dt, k) = f(T, k) - \left( \frac{\partial f}{\partial t} \right)_{t=T} dt. \quad (35)$$

If

$$\left( \frac{\partial f}{\partial t} \right)_{t=T} < 0,$$

then

$$f(T - dt, k) > f(T, k) = kh. \quad (36)$$

The time required for excitation  $T$  is determined by the smallest positive root of (24), i.e., the time at which  $f(t, k)$  first reaches a constant threshold value which is given by  $kh$ . But, according to (36),  $f(t, k)$  must have surpassed its threshold  $kh$  at a time earlier than  $T$ , and it follows that

$$\left( \frac{\partial f}{\partial t} \right)_{t=T} \geq 0. \quad (37)$$

Comparison of (25), (34), and (37) completes the proof that

$$\frac{\partial T}{\partial k} > 0, \quad (38)$$

and thus it follows that the heart rate should be decreased by acetylcholine and increased by sympathin.

Inequality (37) imposes a restriction on  $F$  which may be useful in the future development of the theory. This restriction is seen more clearly if  $f(t, k)$  in equation (26) is differentiated with respect to  $t$ , for then

$$\frac{\partial f}{\partial t} = k \left( F[S(t)] - k e^{-kt} \int_0^t F[S(\theta)] e^{k\theta} d\theta \right), \quad (39)$$

and using (37) and (28), we obtain

$$F[S(T)] > k e^{-kT} \int_0^T F[S(\theta)] e^{k\theta} d\theta = kh. \quad (40)$$

5. *Excessive concentrations of acetylcholine are capable of completely stopping the spontaneous heartbeat* (cf. Evans 1949). If  $F[S(t)]$  is bounded, then  $F[S(\xi_i)]$  is also bounded. Let the upper bound of  $F[S(\xi_i)]$  be given by  $\zeta$ . If the concentration of acetylcholine causes  $k$  to increase monotonically, and if the value of  $k$  surpasses  $\zeta/h$ , then, according to equation (22), the heart will stop beating. This is suggestive of the well-known experimental phenomena in which increasing the concentration of acetylcholine causes the heart rate to slow more and more, but when the concentration gets sufficiently large, the heart suddenly stops altogether.

In the next paper, a particular case will be considered in which explicit assumptions will be made regarding the variation of  $F$  with time, and the variation of  $k$  with the concentrations of the chemical mediators.

I would like to thank Dr. George Karreman and Mr. Clifford Patlak for reading and discussing this paper.

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## THE EFFECT OF ENVIRONMENTAL FACTORS ON THE RATES OF CULTURAL DEVELOPMENTS

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Progress in social and cultural life is initiated by a small group of individuals, who do not follow the socially accepted habits, patterns of behavior, or ideas. Such individuals may be conveniently called nonconformists. The rate of cultural progress depends largely on their number. This number is partly determined by purely biological factors, which result in a certain fraction of individuals being born with the necessary predisposition. Partly, it is determined by the circumstance that the progeny of nonconformists is reared and educated in nonconformist behavior. This latter process requires the possibility for the existing nonconformists to gather together and to form semi-closed social groups. This, in turn, depends to a large extent on the rate of urbanization of the population, which is affected by various environmental factors.

Mathematical expressions are developed which show how these different environmental factors affect the growth of the number of nonconformists, and thus affect the rate of cultural changes. Some very general comparisons with known facts indicate the possibility of future applications of the theory.

The principal result of the study is the fact that social groups with identical biological characteristics may show a great difference in cultural development due to differences in environment.

It probably will be generally agreed that the essence of every cultural development and of progress consists of a gradual freeing of society from old unfounded beliefs, prejudices, and established habits and customs. The cultural importance of habits and customs has been emphasized by anthropologists (Benedict, 1950). Freeing society from the prejudice of superiority of some classes resulted in the abolition of slavery and marked an important milestone on the road of cultural development. The prejudice of racial superiority still exists, though it may be lessening. The freeing of society from the medieval prejudice that free thought and investigation were sins against the church led to a highly increased tempo of development of the natural sciences.

In two preceding papers (Rashevsky 1951b, c; hereinafter referred to as I and II) we have discussed a mechanism by means of which society

gradually frees itself of strongly conditioned beliefs and prejudices. Depending on the distribution in the society of certain psychobiological traits, a certain small fraction of individuals will overcome the early conditioning and social pressure which tend to preserve some established beliefs. Those individuals are thus free from those particular beliefs, and with respect to them they do not behave like the majority of the society. For brevity, we shall call such individuals nonconformists.

The mathematical expression for the fraction  $\alpha$  of nonconformists (II) shows that  $\alpha$  depends, among other things, on such purely biological factors as the average age of the individual in a given society. The quantity  $\alpha$  varies with time, but tends to an asymptotic value, which is almost reached within two or three generations. This asymptotic value of  $\alpha$  is usually too small to have any appreciable effect on the behavior of the majority of the society.

If, however, we assume that the nonconformists, or at least a fixed fraction of them, rear their progeny as nonconformists, then, as we have seen in I, the ratio  $n/N$  of nonconformists to the total population tends to 1 according to the expression [I, equation (25)]

$$\frac{n}{N} = 1 - e^{-\alpha\mu t}, \quad (1)$$

where  $\mu$  is the relative rate of increase of the total population  $N$ . If the death rate is equal to  $\nu$ , then  $N$  varies exponentially according to

$$N = N_0 e^{\beta t}, \quad (2)$$

where  $\beta = \mu - \nu$ .

The constant  $\alpha$  is essentially a biological quantity. It represents approximately the fraction of individuals born in the society who possess psychobiological predispositions which cause them to become nonconformists. The quantity  $n$  is the total number of nonconformists, both the innate ones and those who become nonconformists as a result of their upbringing and education. Though  $\alpha$  depends on the age at which a prejudice begins to be conditioned (Rashevsky, 1951c), nevertheless it does not vary a great deal, while  $n$  increases according to (1).

Let us consider somewhat more closely the derivation of equation (1). If a fraction  $\alpha$  of the newborn individuals eventually becomes nonconformists, and if all individuals born of nonconformist parents and reared as nonconformists permanently so remain, then we have:

$$\frac{dn}{dt} = \beta n + \alpha\mu (N - n). \quad (3)$$

Introducing expression (2) into (3), and integrating with the initial condition

$$n = 0 \text{ for } t = 0, \quad (4)$$

we obtain equation (1).

The assumption which leads to (3) tacitly implies that both parents are nonconformists. It also implies that any nonconformist parents can rear their offspring as nonconformists, in spite of the social pressure of all other individuals. Clearly this is not realistic. If  $\alpha$  is very small—say,  $\sim 0.01$  or less—then, in a society with a small density of population and a uniform spatial distribution, the probability of a nonconformist marrying another nonconformist is also very small. Even if this happens, their children are exposed to the influence of the average members of the society, and rearing them as nonconformists becomes practically impossible. In order to satisfy the assumptions implied in the derivation of (1), two conditions are necessary. First, the population density must be large enough to bring a sufficient number of nonconformists within a sufficient spatial proximity to each other, even for a small  $\alpha$ . Second, the absolute number of nonconformists who do come together must be sufficiently large to form a more or less closed group, in which the children may be reared with a minimum disturbance from the rest of the society.

If, as is usually the case, the individuals of a society are not distributed spatially uniformly, but divide into urban and rural populations, then it may well happen that while the conditions for (1) are not satisfied in the rural population, they are satisfied in the urban. If that is the case, then the following happens. Let  $N_u$  denote the total urban population. Of the  $\alpha N$  nonconformist individuals born in the society as a whole, only  $\alpha N_u/N$  will be able to rear their progeny as nonconformists. This will have the same effect as if we substitute in equations (3) and (1) for  $\alpha$  the value

$$\alpha_e = \frac{\alpha N_u}{N}, \quad (5)$$

which we may call the *effective*  $\alpha$ . With these simple assumptions, the larger  $N_u/N$  is, in other words, the larger the urbanization, the larger the effective  $\alpha_e$  and the faster the spread of nonconformism in the society.

This picture is still too oversimplified. We shall now introduce several complications, one at a time, and thus arrive gradually at more realistic results.

First, we observe that the ratio  $N_u/N$  is not constant but increases with  $N$  (Rashevsky, 1947, chap. x; 1951, chap. xviii). The form of the relation between  $N_u/N$  and  $N$  depends on the assumptions which we make about

the shift between rural and urban population. As an illustration only, we shall use here one of the simplest possible assumptions made before, the consequences of which lead to agreement with some observed data (Rashevsky, 1947, chap. x; 1951, chap. xviii).

As before, we shall assume that the equilibrium between rural and urban population is determined by the equality of the production per capita. We consider that the rural production per capita is of the form

$$p_r = \frac{a_1}{N_r + a_2}, \quad (6)$$

where  $a_1$  and  $a_2$  are constants, and  $N_r$  denotes the total rural population. The total urban production per capita is considered as constant. Putting

$$a_2 - \frac{a_1}{p_u} = -c^2, \quad (7)$$

we obtain

$$\frac{N_u}{N} = 1 - \frac{c^2}{N}, \quad (8)$$

or

$$N_u = N - c^2. \quad (9)$$

Let us consider the possible meanings of the constants  $a_1$ ,  $a_2$ , and  $c^2$ , and their dependence on other factors.

If  $f$  denotes the fertility of the soil per unit area, that is, the maximum possible yield; if  $S$  denotes the total rural area; and if  $a$  denotes the maximum area which one individual can cultivate, then for very small values of  $N_r$ , when everyone has much more land available than he can cultivate, we have roughly

$$p_r = af. \quad (10)$$

When  $N_r \gg S/a$ , the area available for each individual is  $S/N_r$ , and we have

$$p_r = \frac{Sf}{N_r}. \quad (11)$$

These two limiting cases are obtained from (6) if we put

$$a_1 = Sf; \quad a_2 = \frac{S}{a}. \quad (12)$$

We explicitly neglect in this crude zeroth approximation the diversification of rural activities, such as agriculture, cattle breeding, etc.

As regards  $p_u$ , it may depend on the following factors. First, we notice that the less the fertility  $f$ , the more inducement an individual finds to move to the city. With smaller  $f$ , the rural population has to devote all of

its time and effort to agricultural pursuits and cannot take care of other needs, such as production of clothing, building materials, etc. More of these items are produced in the city. The existence of neighboring countries with high agricultural production will tend to increase  $p_u$ . The reason for this is that such countries are likely to be good markets for items produced in the cities. Climatic conditions also affect  $p_u$ . Thus in a very warm climate, where production of clothing and shelter is a secondary activity and is not essential for life, there is no need for manufacturing enterprises, which are located in cities. Larger available mineral resources also increase  $p_u$ , since mining and metallurgical activities are definitely city occupations. As a crude approximation we shall assume all the relations to be linear within a certain range. Denoting by  $c_1, c_2, c_3, c_4$ , and  $c_5$  five positive constants, by  $N_a$  the population of neighboring agricultural countries, by  $\tau$  the average yearly temperature of the region, and by  $M$  the mineral resources, we may put

$$p_u = c_1 - c_2 f + c_3 N_a - c_4 \tau + c_5 M. \quad (13)$$

From (7), (12), and (13) we find

$$c^2 = \frac{Sf}{c_1 - c_2 f + c_3 N_a + c_4 \tau + c_5 M} - \frac{S}{a}. \quad (14)$$

Assuming an exponential increase of the population, we obtain, by introducing (2) into (8) and the latter into (5):

$$a_e = a \left( 1 - \frac{c^2}{N_0} e^{-\beta t} \right). \quad (15)$$

Thus  $a_e < a$ , but tends asymptotically to the "biological" value  $a$ .

Now, however,  $a_e$  is a function of time. Substitution of  $a_e$  for  $a$  in equation (3) now changes the form of the equation, and we do not obtain expression (1) now upon integration. The differential equation (3) still remains linear and can be solved by standard methods. The solution, however, leads to integrals of the form:

$$\frac{n}{N} = 1 - e^{-a\mu t + (ac^2/\beta N_0)(1-e^{-\beta t})}. \quad (16)$$

It is readily seen that expression (15) leads to a more decelerated rate of increase of nonconformists than that given by (1). In line with what we said in the introductory pages, we may say that expression (15) leads to a lower speed of cultural development.

Although the assumptions made here are very inaccurate and were used only as an illustration of the method, it may be worth discussing equations

(14) and (15). As we see,  $c^2$  increases with  $S$ ,  $f$ ,  $\tau$ , and  $a$ , and decreases with  $N_0$  and  $M$ . Hence for the same span of development time we would expect very large countries with fertile soil to be more retarded than others. A large  $N_0$  means a larger average  $a_e$ , but, if  $\beta$  is the same, it means at any time a greater population  $N$ . Hence we should expect a retardation in countries with very large areas. A warm climate also reduces  $a_e$ . Larger mineral resources increase  $a_e$ . We actually see that the small, highly urbanized city states of Greece exhibited a very rapid cultural development. The Western European countries, smaller both in area and population than Russia, showed a much more rapid progress both in socio-political institutions and in technology than did Russia. A comparison of Western Europe with China and India also shows the same trend. Factors which affect  $a_e$  in opposite directions may affect each other. The Eskimos are characterized by small  $N_0$ , very small  $\tau$ , and negligible  $f$ . But then  $N_0$  and  $M$  are also near zero. The obviously small value of their  $a_e$  need not, therefore, be surprising.

We now shall introduce the next complication. Equation (5) is obtained under the assumption that in the cities both the requirement of the necessary minimum density of the nonconformists and the requirement of the necessary minimum number to form a semi-closed group are satisfied.

The first assumption is more likely to be realistic. While cities vary in their population density, this variation is not as large as the variation in population density between city and country. The discussion of the possible effect of the density of city population requires a further elaboration of the theory of formation of cities, and for the present we shall not consider it.

The second assumption can be readily generalized at this time. Let the necessary minimum number of nonconformists be  $g$ . This situation is quite likely: although for a particular society the total urban population  $N_u > g$ , the number of cities is so large that in each city the population is less than  $g$ . Consider first the unrealistic case in which all cities are of the same average size  $\bar{n}_u$ . Then  $a_e$  is different from zero if, and only if,

$$a \bar{n}_u \geq g. \quad (17)$$

The problem of the average size of cities is closely connected with the problem of distribution of city sizes, and an approach to it has been suggested elsewhere (Rashevsky, 1947, chaps. xi-xii). Here, again as an illustration, we shall consider a much cruder approach to the problem.

Since there must be a constant interchange of goods between city and country, the number  $m$  of cities is roughly determined by the area  $s$  from

which supplies can still be received. In a very large country if all the urban population should be concentrated in one city, it could not exchange the necessary goods with the whole rural population. The size of the area  $s$  depends on many factors, such as roads, rivers, etc. The area  $s$  increases with increasing improvement in methods of communication, and is, therefore, itself a function of the technological development of the country. For the present we shall consider it, however, as constant. The area  $s$  may depend also on the *specific seashore line*  $l_s$  of the country, that is, the ratio of the length of the seashore line to the area. The larger  $l_s$ , the more cities will be located on the seashore. Sea communication in the past has always been easier than land communication. Greater distances from the city can be more easily reached when  $l_s$  is large. We may put

$$s = s_0 + kl_s. \quad (18)$$

We have approximately

$$m = \frac{S}{s}, \quad (19)$$

and

$$\bar{n}_u = \frac{N_u}{m} = \frac{N_u s}{S}. \quad (20)$$

From (17) and (20) we find

$$\frac{aN_u s}{S} \geq g, \quad (21)$$

or

$$N_u \geq \frac{Sg}{a s}. \quad (22)$$

From (2) and (9) we have

$$N_u = N_0 e^{\beta t} - c^2. \quad (23)$$

Setting the right side of (23) equal to the right side of (22) and solving for  $t$ , we find the moment  $t^*$  at which (22) begins to be satisfied. We thus obtain

$$t^* = \frac{1}{\beta} \log \left( \frac{Sg}{N_0 a s} + \frac{c^2}{N_0} \right). \quad (24)$$

Prior to  $t^*$  we have  $a_e = 0$ , and the number of nonconformists remains constant and small, equal to  $aN$ . This does not necessarily mean any lack of progress of culture with time, but progress will be very small due to individual efforts of single nonconformists. Development of arts can proceed under those conditions much more readily than development of science and technology (Rashevsky, 1947, p. 178). For  $t > t^*$  the situation changes. Now  $a_e$  is given by expression (15), and the number of nonconformists increases.

Equation (24), together with (14), shows that  $t^*$  increases with  $S$ ,  $\tau$ , and  $f$ , and decreases with  $N_0$ ,  $N_a$ , and  $M$ . Thus the same factors which increase or decrease the value of  $\alpha_e$  correspondingly shorten or lengthen the initial time lag  $t^*$  of intensive development. This of course enhances the over-all effect of those factors.

As the next step we shall consider the fact that the cities are not all of the same size. As we said above, a general approach to the problem of the distribution of sizes of cities has been suggested elsewhere (Rashevsky, 1947). Let us see what effect such a distribution will have on  $\alpha_e$  and  $t^*$ .

Let  $m(n_u)dn_u$  denote the number of cities with populations between  $n_u$  and  $n_u + dn_u$ . We have

$$\int_0^\infty m(n_u) dn_u = m. \quad (25)$$

Only in those cities will groups of nonconformists be formed for which

$$\alpha n_u > g, \quad \text{or} \quad n_u > \frac{g}{\alpha}. \quad (26)$$

The total number of nonconformists in such groups is

$$\int_{g/\alpha}^\infty \alpha n_u m(n_u) dn_u. \quad (27)$$

Hence

$$\alpha_e = \frac{\alpha}{N} \int_{g/\alpha}^\infty n_u m(n_u) dn_u. \quad (28)$$

Let us consider again, as an illustration only, the following example. Let  $m(n_u)$  be of the form:

$$m(n_u) = \frac{m}{\bar{n}_u} e^{-n_u/\bar{n}_u}, \quad (29)$$

where  $\bar{n}_u$  is, as before, the average size of the city. From (20) and (29) we find

$$m(n_u) = \frac{mS}{N_u s} e^{-(S/N_u s)n_u}. \quad (30)$$

Introducing (30) into (28) and making use of (19), we find

$$\alpha_e = \left( \frac{Sg}{N_s} + \frac{N_u}{N} \right) e^{-Sg/N_u s}. \quad (31)$$

For  $N_u = 0$ ,  $\alpha_e = 0$ . We see that  $\alpha_e$  again increases with  $N_u$ ; hence it again decreases with  $c^2$ . The effect of the environmental factors is qualitatively the same as before but quantitatively more complex. Moreover the new factor  $s$  is introduced, and, because of (18), this introduces  $l_s$ . We see that  $\alpha_e$  increases with  $l_s$ . We may notice that Western Europe has the largest  $l_s$  of all other continental parts of the world.

If  $n_m$  is the population of the largest city, then we may say that the number of cities whose population lies between  $n_m$  and  $\infty$  is 1. This defines  $n_m$  as the root of the equation

$$\int_{n_m}^{\infty} m(n_u) dn_u = 1. \quad (32)$$

Introducing (30) into (32) we find

$$n_m = \frac{N_u s}{S} \log \frac{S}{s}. \quad (33)$$

The value of  $a_e$  will remain zero as long as

$$a n_m < g, \quad \text{or} \quad n_m < \frac{g}{a}. \quad (34)$$

Introducing (23) into (33), equating the latter to  $g/a$ , and solving for  $t$ , we find the time lag  $t^*$

$$t^* = \frac{1}{\beta} \left[ \log \frac{S g}{N_0 a s \log(S/s)} + \frac{c^2}{N_0} \right]. \quad (35)$$

The relation is similar to (24).

Since the formation of groups of nonconformists begins in the largest city, cultural developments will spread also from the largest cities. The smaller "provincial" towns and the country are affected later. This conclusion seems to be borne out by history.

Because of the crude approximations and oversimplifications used above, we cannot draw any definite conclusions from the paper which could be subject to direct verification. The importance of the above results lies, however, in the fact that they show the possibility of large disparities of rates of cultural developments of peoples whose biological characteristics are identical. This does not prove, of course, that all the observed cultural disparities are of an environmental nature. It shows, however, that environment may be a sufficient cause of those disparities.

The author is indebted to Dr. George Karreman for a critical discussion of the paper.

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## ON SOME PROBLEMS OF RANDOM NETS

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The probability problems connected with random nets are restated as probabilities of drawings from an urn containing black and white balls. A partial difference equation is obtained and its solution is given. For large nets a series expression is obtained for the connectivity  $\gamma$ , and this is shown to be equivalent to the transcendental equation obtained by R. Solomonoff and A. Rapoport (1951).

*Introduction.* A random net has been defined by Rapoport as a set of  $n$  points, each of which is connected by directed line segments to  $a$  points of the set chosen at random. The weak connectivity  $\gamma$  is then the expected fraction of the points which can be reached by tracing along the line segments starting from a randomly chosen initial point. Solomonoff and Rapoport (*loc. cit.*) have given various interpretations of this model, and also an approximate solution for  $\gamma$  which is equivalent to the one derived below when  $n$  is large. Solomonoff (1952) has also given an exact method using Markov chains, but the required calculations are very involved and do not lead to an explicit expression for  $\gamma$ .

We restate the problem as an urn problem. An urn contains  $n$  balls,  $w$  being white and  $n-w$  black. There is a player who has  $s$  tickets. He pays one ticket for the right to draw a ball at random from the urn. If the ball drawn is white, he receives  $a$  additional tickets, if black he receives nothing. The ball drawn is always replaced by a black ball. Drawings continue until  $s = 0$ .

The random net interpretation of this game is that black balls represent points already reached in the tracing process, white balls points not previously reached, and the tickets are the number of lines, emanating from previously reached points, which have not yet been traced.\*

\* In the random net interpretation we may want to exclude the possibility of a line from any point directly back to itself. This simply requires that we omit one black ball from the urn; the omitted black ball then corresponds to the point from which lines are being traced.

Now let  $E(w, s)$  be the expected number of white balls at the end of the drawings, when the drawings started with  $w$  white balls and  $s$  tickets. Then the weak connectivity is

$$\gamma = 1 - \frac{E(n, 1)}{n}. \quad (1)$$

Also, let  $p(w, s, u)$  be the probability that the drawings end with  $u$  white balls, when they started with  $w$  white balls and  $s$  tickets. Then the strong connectivity, or probability of no white balls remaining from a start with all white balls and one ticket, is  $p(n, 1, 0)$ .

The expected value and probabilities are related by

$$E(w, s) = \sum_{u=0}^w u p(w, s, u), \quad (2)$$

since

$$p(w, s, u) = 0 \quad \text{for} \quad u > w. \quad (3)$$

Equation (3) states that the number of white balls cannot increase during the drawings.

*Difference equations.* We now derive the difference equations for the  $p(w, s, u)$  by considering the possible outcomes of successive draws. In order to have  $u = w$ , i.e., no change in number of white balls, only black balls must be drawn, so that

$$p(w, s, w) = \left(1 - \frac{w}{n}\right) p(w, s-1, w), \quad (4)$$

since  $1 - w/n$  is the probability of drawing a black ball. For  $u < w$ ,

$$p(w, s, u) = \left(1 - \frac{w}{n}\right) p(w, s-1, u) + \left(\frac{w}{n}\right) p(w-1, s-1+u, u). \quad (5)$$

This equation states that the probability of ending with  $u$  white balls is equal to the probability of a black ball on the first draw, multiplied by the probability of ending with  $u$  white from a start with  $w$  white and one less ticket, *plus* the probability of white on the first draw, multiplied by the probability of ending with  $u$  white from a start with  $w-1$  white and  $u-1$  additional tickets.

In (4) and (5) we must have  $s > 0$ . For  $s = 0$ ,

$$\begin{aligned} p(w, 0, u) &= 0, & \text{for } u &\neq w, \\ &= 1, & \text{for } u &= w. \end{aligned} \quad (6)$$

The values of  $p(w, s, u)$  for  $w = 0$ , as follow from (4), (5), and (6), are

$$\begin{aligned} p(0, s, u) &= 0, & \text{for } u > 0, \\ &= 1, & \text{for } u = 0. \end{aligned} \quad (7)$$

We are mainly interested in the connectivity, so we now derive the difference equation for the expected number of white balls. From (2), (4), and (5),

$$\begin{aligned} E(w, s) = \sum_{u=0}^w u p(w, s, u) &= \left(1 - \frac{w}{n}\right) \sum_{u=0}^w u p(w, s-1, u) \\ &\quad + \left(\frac{w}{n}\right) \sum_{u=0}^{w-1} u p(w-1, s-1+u, u), \end{aligned}$$

or

$$E(w, s) = \left(1 - \frac{w}{n}\right) E(w, s-1) + \left(\frac{w}{n}\right) E(w-1, s-1+a). \quad (8)$$

The boundary values for this equation are, from (6) and (7),

$$E(w, 0) = w, \quad (9)$$

$$E(0, s) = 0. \quad (10)$$

*Solution of difference equation.* The difference equations for  $p$  and  $E$ , (5) and (8), are of the same form, so we give the solution for  $E(w, s)$ . This can be arrived at by fixing  $w$  and solving the ordinary difference equations in  $s$  for  $E(1, s)$ ,  $E(2, s)$ , . . . . The form of the first few solutions suggests a general form, (16), for  $E(w, s)$ , containing undetermined coefficients. The validity of this general form and the equations determining the coefficients can then be obtained by standard methods for ordinary difference equations (Milne-Thompson, 1933).

From (8), (9), and (10)

$$E(1, s) = \left(1 - \frac{1}{n}\right) E(1, s-1), \quad E(1, 0) = 1, \quad (11)$$

so that we have immediately

$$E(1, s) = \left(1 - \frac{1}{n}\right)^s. \quad (12)$$

Putting this value in the equation for  $E(2, s)$ ,

$$E(2, s) = \left(1 - \frac{2}{n}\right) E(2, s-1) + \left(\frac{2}{n}\right) \left(1 - \frac{1}{n}\right)^{s-1+a}. \quad (13)$$

The solution of this equation may be written as

$$E(2, s) = A_2 \left(1 - \frac{2}{n}\right)^s + 2 \left(1 - \frac{1}{n}\right)^{s+a},$$

where  $A_2$  is a constant to be determined from  $E(2, 0) = 2$ , so that

$$E(2, s) = 2 \left(1 - \frac{1}{n}\right)^{s+a} + 2 \left[1 - \left(1 - \frac{1}{n}\right)^a\right] \left(1 - \frac{2}{n}\right)^s. \quad (14)$$

Similarly,

$$\begin{aligned} E(3, s) = & 3 \left(1 - \frac{1}{n}\right)^{s+2a} + 6 \left[1 - \left(1 - \frac{1}{n}\right)^a\right] \left(1 - \frac{2}{n}\right)^{s+a} \\ & + 3 \left\{1 - \left(1 - \frac{1}{n}\right)^{2a} - 2 \left[1 - \left(1 - \frac{1}{n}\right)^a\right] \left(1 - \frac{2}{n}\right)^a\right\} \left(1 - \frac{3}{n}\right)^s. \end{aligned} \quad (15)$$

This suggests that we take as the general form for  $E(w, s)$

$$E(w, s) = \sum_{i=1}^w c_i \left(1 - \frac{i}{n}\right)^{s+(w-i)a}, \quad (16)$$

where the  $c_i$  are independent of  $s$ . When we insert this expression for  $E(w-1, s-1+a)$  in (8), and solve the resulting difference equation in  $s$ ,

$$E(w, s) = A_w \left(1 - \frac{w}{n}\right)^s + \sum_{i=1}^{w-1} c_i \frac{w}{w-1} \left(1 - \frac{i}{n}\right)^{s+(w-i)a}.$$

Then (9) gives

$$w = A_w + \sum_{i=1}^{w-1} c_i \frac{w}{w-1} \left(1 - \frac{i}{n}\right)^{(w-i)a}.$$

Now we can see that if we put  $c_i = b_i \binom{w}{i}$ ,  $b_i$  will be independent of  $w$ , and the solution can be written

$$E(w, s) = \sum_{i=1}^w b_i \binom{w}{i} \left(1 - \frac{i}{n}\right)^{s+(w-i)a}, \quad (17)$$

with

$$w = \sum_{i=1}^w b_i \binom{w}{i} \left(1 - \frac{i}{n}\right)^{(w-i)a}, \quad w = 1, 2, \dots, n-1. \quad (18)$$

This can, of course, be verified by substitution in (8) and (9).

The  $b_i$  depend on  $n$  and  $a$  only. The first three values, as can be obtained from (18) or from (12), (14), and (15), are

$$\begin{aligned} b_1 &= 1, \\ b_2 &= 2 \left[ 1 - \left( 1 - \frac{1}{n} \right)^a \right], \\ b_3 &= 3 \left\{ 1 - \left( 1 - \frac{1}{n} \right)^{2a} - 2 \left[ 1 - \left( 1 - \frac{1}{n} \right)^a \right] \left( 1 - \frac{2}{n} \right)^a \right\}. \end{aligned} \quad (19)$$

To obtain an explicit expression for  $E(w, s)$ , we can solve the equations (18) in succession for  $b_1, b_2, \dots, b_w$  and then substitute in (17), or we can express  $E(w, s)$  directly by writing the solution of the  $w + 1$  linear equations (18) and (17) for  $b_1, b_2, \dots, b_w, E(w, s)$ . The determinant of this set of equations is readily seen to be  $-1$  since the coefficient of  $b_i$  in the  $i$ th equation of (18) is 1, while the  $b$ 's with higher index all have zero coefficients in this equation.

We are interested mainly in  $E(n, 1)$  which gives  $\gamma$  by (1). Writing

$$x_i = \left( 1 - \frac{i}{n} \right)^a, \quad (20)$$

and noticing that  $b_n$  has zero coefficient in (17), we have

$$E(n, 1) = \sum_{i=1}^{n-1} b_i \binom{n}{i} x_i^{n-i} \left( 1 - \frac{i}{n} \right) = \sum_{i=1}^{n-1} b_i \binom{n-1}{i} x_i^{n-i}. \quad (21)$$

This equation with the  $n - 1$  equations of (18) gives the following determinant for  $E(n, 1)$ :

$$\begin{array}{cccccc} -E(n, 1) = & & & & & \\ \left| \begin{array}{cccccc} 1 & 0 & 0 & \cdots & 0 & 1 \\ 2x_1 & 1 & 0 & \cdots & 0 & 2 \\ 3x_1^2 & \binom{3}{2}x_2 & 1 & \cdots & 0 & 3 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ (n-2)x_1^{n-3} & \binom{n-2}{2}x_2^{n-4} & \binom{n-2}{3}x_3^{n-5} & \cdots & 1 & 0 & n-2 \\ (n-1)x_1^{n-2} & \binom{n-1}{2}x_2^{n-3} & \binom{n-1}{3}x_3^{n-4} & \cdots & (n-1)x_{n-2} & 1 & n-1 \\ (n-1)x_1^{n-1} & \binom{n-1}{2}x_2^{n-2} & \binom{n-1}{3}x_3^{n-3} & \cdots & (n-1)x_{n-2}^2 & x_{n-1} & 0 \end{array} \right| \end{array} \quad (22)$$

For example, either from this determinant or (19) and (21)

$$E(4, 1) = 3 \left(\frac{3}{4}\right)^{3a} + 6 \left[1 - \left(\frac{3}{4}\right)^a\right] \left(\frac{2}{4}\right)^{2a} \\ + 3 \left\{1 - \left(\frac{3}{4}\right)^{2a} - 2 \left[1 - \left(\frac{3}{4}\right)^a\right] \left(\frac{2}{4}\right)^a\right\} \left(\frac{1}{4}\right)^a,$$

and, more generally, the first three terms of  $E(n, 1)$  are

$$E(n, 1) = (n-1) \left[ \left(1 - \frac{1}{n}\right)^{(n-1)a} \right. \\ + (n-2) \left[ 1 - \left(1 - \frac{1}{n}\right)^a \right] \left(1 - \frac{2}{n}\right)^{(n-2)a} \\ \left. + \frac{(n-2)(n-3)}{2} \left\{ 1 - \left(1 - \frac{1}{n}\right)^{2a} \right. \right. \\ \left. \left. - 2 \left[ 1 - \left(1 - \frac{1}{n}\right)^a \right] \left(1 - \frac{2}{n}\right)^a \right\} \left(1 - \frac{3}{n}\right)^{(n-3)a} + \dots \right]. \quad (23)$$

*Modified equation for coefficients,  $b_i$ .* The expression for  $E(n, 1)$  becomes very complicated as  $n$  increases. For  $a = 1$ , it is possible to obtain a simple expression directly (Rapoport, 1948), which is shown below to be a special case of (21). For  $a > 1$ , we consider the limit as  $n \rightarrow \infty$ , since this is the case of principal interest.

For these purposes we first obtain a modified form of equation (18) for the  $b_i$ , which is given in (26) below.

In (18), multiply each equation up to  $w = v$  ( $v < n$ ) by

$$(-1)^{w-1} \binom{v}{w},$$

and add, then,

$$S_v = \sum_{w=1}^v (-1)^{w-1} \binom{v}{w} w = \sum_{w=1}^v (-1)^{w-1} \binom{v}{w} \sum_{i=1}^w b_i \binom{w}{i} x_i^{n-i}. \quad (24)$$

Now

$$\sum_{w=1}^v (-1)^{w-1} \binom{v}{w} w = 1, \quad \text{for } v = 1, \\ = 0, \quad \text{for } v > 1,$$

as can be seen by noting that this sum is  $(-1)^{v-1} \Delta^v 0$ . Here we are using difference notation and this is a special case of the formula (Milne-Thompson, *loc. cit.*)

$$\Delta^m t^r = \sum_{i=0}^m (-1)^{m-i} \binom{m}{i} (t+i)^r. \quad (25)$$

In the double sum on the right in (24), we interchange the order of summation, and obtain

$$\begin{aligned}
 S_v &= \sum_{i=1}^v b_i \sum_{w=i}^v (-1)^{w-i} \binom{v}{w} \binom{w}{i} x_i^{w-i} \\
 &= \sum_{i=1}^v b_i \sum_{j=0}^{v-i} (-1)^{i+j-1} \binom{v}{i+j} \binom{i+j}{i} x_i^j \\
 &= \sum_{i=1}^v (-1)^{i-1} \binom{v}{i} b_i \sum_{j=0}^{v-i} (-1)^j \binom{v-i}{j} x_i^j \\
 &= \sum_{i=1}^v (-1)^{i-1} \binom{v}{i} b_i (1-x_i)^{v-i}.
 \end{aligned}$$

We finally have, writing  $w$  for  $v$ ,

$$\begin{aligned}
 \sum_{i=1}^w (-1)^{i-1} b_i \binom{w}{i} (1-x_i)^{w-i} &= 1, & w &= 1, \\
 &= 0, & w &= 2, 3, \dots, n-1.
 \end{aligned} \tag{26}$$

Now for  $a = 1$ ,  $1 - x_i = 1/n$ , and from this it readily follows that

$$b_i = \left(\frac{i}{n}\right)^{i-1} \tag{27}$$

by induction, using (26) and (25).

Using (27) to evaluate  $\gamma$  for  $a = 1$ , we obtain after some manipulation

$$\gamma = \frac{(n-1)!}{n^n} \sum_{k=0}^{n-1} \frac{n^k}{k!}, \tag{28}$$

which agrees with the result obtained by Rapoport (1948).

*The limit as  $n \rightarrow \infty$ , for  $a > 1$ .* We will first obtain the initial term for the expansion of  $b_i$  in powers of  $1/n$ . From (26),  $b_i$  is a polynomial in  $1/n$ . Let

$$b_i = \sum_{k=0}^{K_i} b_{i,k} n^{-k}. \tag{29}$$

We show that

$$b_{i,k} = 0, \quad \text{for } k < i-1, \tag{30}$$

$$b_{i,i-1} = (ia)^{i-1}. \tag{31}$$

From (19) it can be seen that this is true for  $i = 1, 2, 3$ . Assuming then that for  $i = 1, \dots, w-1$

$$b_i = \left(\frac{ia}{n}\right)^{i-1} + \frac{A_i}{n^i},$$

where  $A_i$  is a polynomial in  $1/n$ , and writing

$$1 - x_i = 1 - \left(1 - \frac{i}{n}\right)^a = \frac{ia}{n} + \frac{y_i}{n^2},$$

where  $y_i$  is also a polynomial in  $1/n$ , we have from (26)

$$\begin{aligned} b_w &= \sum_{i=1}^{w-1} (-1)^{w+i-1} \binom{w}{i} \left[ \left(\frac{ia}{n}\right)^{i-1} + \frac{A_i}{n^i} \right] \left[ \frac{ia}{n} + \frac{y_i}{n^2} \right]^{w-i} \\ &= \sum_{i=1}^{w-1} (-1)^{w+i-1} \binom{w}{i} \left(\frac{ia}{n}\right)^{i-1} \left(\frac{ia}{n}\right)^{w-i} + T_i, \end{aligned}$$

where  $T_i$  is a polynomial in  $1/n$  which starts with a term in  $1/n^w$ . This proves (30). Also

$$b_{w, w-1} = a^{w-1} \sum_{i=1}^{w-1} (-1)^{w+i-1} \binom{w}{i} i^{w-1},$$

but, using (25),

$$\sum_{i=1}^{w-1} (-1)^{w+i-1} \binom{w}{i} i^{w-1} - w^{w-1} = 0,$$

so

$$b_{w, w-1} = (aw)^{w-1};$$

proving (31).

We can now obtain an expression for  $\gamma$  for large  $n$ . In

$$\gamma = 1 - \frac{E(n, 1)}{n} = 1 - \sum_{i=1}^{n-1} \frac{b_i}{n} \binom{n-1}{i} x_i^{n-1}, \quad (32)$$

we have, as  $n \rightarrow \infty$  from (31),

$$\frac{b_i}{n} \sim \frac{(ia)^{i-1}}{n^i},$$

and also

$$\binom{n-1}{i} \sim \frac{n^i}{i!}.$$

Here  $f(n) \sim g(n)$  means  $f(n)/g(n) \rightarrow 1$  as  $n \rightarrow \infty$ . Hence

$$\frac{b_i}{n} \binom{n-1}{i} \sim \frac{(ia)^{i-1}}{i!}.$$

Also

$$x_i^{n-i} = \left(1 - \frac{i}{n}\right)^{(n-i)a} \rightarrow e^{-ia}.$$

This indicates that as  $n \rightarrow \infty$ , we have

$$\gamma = 1 - e^{-a} \sum_{i=1}^{\infty} \frac{(ia e^{-a})^{i-1}}{i!}. \quad (33)$$

By examining the ratio of successive terms, it is easily shown that this series converges when  $ae^{-a} < e^{-1}$ , that is, when  $a > 1$ .

This is not a complete proof, because while we have shown that each term in (32) approaches the corresponding term of (33), it does not follow that the sum in (32) has for its limit the series in (33). A direct proof seems to present difficulties so we approach the problem from a different direction.

Solomonoff and Rapoport (*loc. cit.*) have given the following equation for  $\gamma$ :

$$\gamma = 1 - e^{-a\gamma}, \quad (34)$$

which is valid for large  $n$  (Rapoport, 1951). This can be converted into a series for  $\gamma$  in terms of  $a$  by using Lagrange's formula (Goursat, 1927). Lagrange's formula gives for

$$y = a + x\varphi(y)$$

the following series in  $x$ :

$$y = a + \sum_{i=1}^{\infty} \frac{x^i}{i!} \frac{d^{i-1}}{da^{i-1}} [\varphi(a)^i].$$

To apply this to (34), we make a change of variables

$$y = a(1 - \gamma),$$

$$x = ae^{-a};$$

then (34) becomes,

$$y = xe^y,$$

and applying Lagrange's formula gives

$$\begin{aligned} y &= \sum_{i=1}^{\infty} \frac{x^i}{i!} \left[ \frac{d^{i-1}}{dx^{i-1}} e^{ix} \right]_{x=0} \\ &= x \sum_{i=1}^{\infty} \frac{(ix)^{i-1}}{i!}. \end{aligned}$$

Replacing  $x$  and  $y$  by  $a$  and  $\gamma$  we obtain (33) again.

*Strong connectivity.* The probabilities  $p(w, s, u)$  can be calculated by the same method as was used for the expected value. We will not give details but merely state the results for  $p(w, s, 0)$ :

$$p(w, s, 0) = 1 - \sum_{i=1}^w h_i \binom{w}{i} \left(1 - \frac{i}{n}\right)^{s+(w-i)a},$$

with

$$\sum_{i=1}^w h_i \binom{w}{i} \left(1 - \frac{i}{n}\right)^{(w-i)a} = 1, \quad (35)$$

and

$$\lim_{n \rightarrow \infty} h_i = (-1)^{i-1}.$$

It can be shown that the strong connectivity  $p(n, 1, 0)$  approaches zero as  $n \rightarrow \infty$ .

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